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THE UNIVERSITY OF ALBERTA

TAXONOMY AND ECOLOGY OF GASTRO-INTESTINAL HELMINTHS IN PIKAS OF NORTH AMERICA

by

RUSSELL PHILIP HOBBS (C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Taxonomy and Ecology of Gastro-Intestinal Helminths in Pikas of North America" submitted by Russell Philip Hobbs in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

Date APRIL 19, 1976

ABSTRACT

Five helminth species, *Schizorchis caballeroi*, *Eugenuris talkeetnaeuris*, *Labiostomum rauschi*, *Cephaluris alaskensis*, and *C. coloradensis* inhabit *Ochotona collaris* individuals collected from the Ogilvie Mountains, Yukon Territory; and seven, *S. caballeroi*, *Graphidiella ochotonae*, *Murielus harpespiculus*, *Eugenuris* sp. A, *L. coloradensis*, *C. alaskensis*, and *C. coloradensis* inhabit *O. princeps* individuals from the Rocky Mountains of southwestern Alberta. Distinguishing characteristics and host relationships of species in the six genera of helminths are critically reviewed.

Frequencies of helminth intensities approximate the negative binomial distributions, which implies clumping, such that a high proportion of individuals are distributed among relatively few host individuals. The clumping was only partly explained by seasonality, host-sex or host-age related resistance or specificity, and locational differences in abundance. Clumping of infective stages, and interspecific interactions appear to be the major causes of clumping in the definitive hosts.

Abundances of the trichostrongyloids *G. ochotonae* and *M. harpespiculus* exhibit sex-related seasonal fluctuations, which may be related to stress; the highest intensities are found in hosts which may be the most stressed. Juvenile

pikas do not acquire helminth infections until an age of about 40 days, but rapidly pick up helminths after that time. Abundances of some helminth species vary between geographic localities, indicating that pika populations have an island-like distribution.

The community system of helminths in pikas is an old one. The oldest pika helminths (*G. ochotonae*, and pinworms of the subfamily Labiostominae), appear to have the most sophisticated means of avoiding competition: selective site segregation. *Schizorchis caballeroi* is probably the most recent acquisition to the community system, and is the one most affected by interactive site segregation.

Known distributions of helminth species of pikas, support the current hypothesis that the North American pikas are derived from a single ancestral species, which migrated across Beringia during the Illinoian glaciation. This species rapidly spread south, and later was split into two groups by the barrier caused by the merging of the Cordilleran and Laurentide ice sheets during the Wisconsin glaciation.

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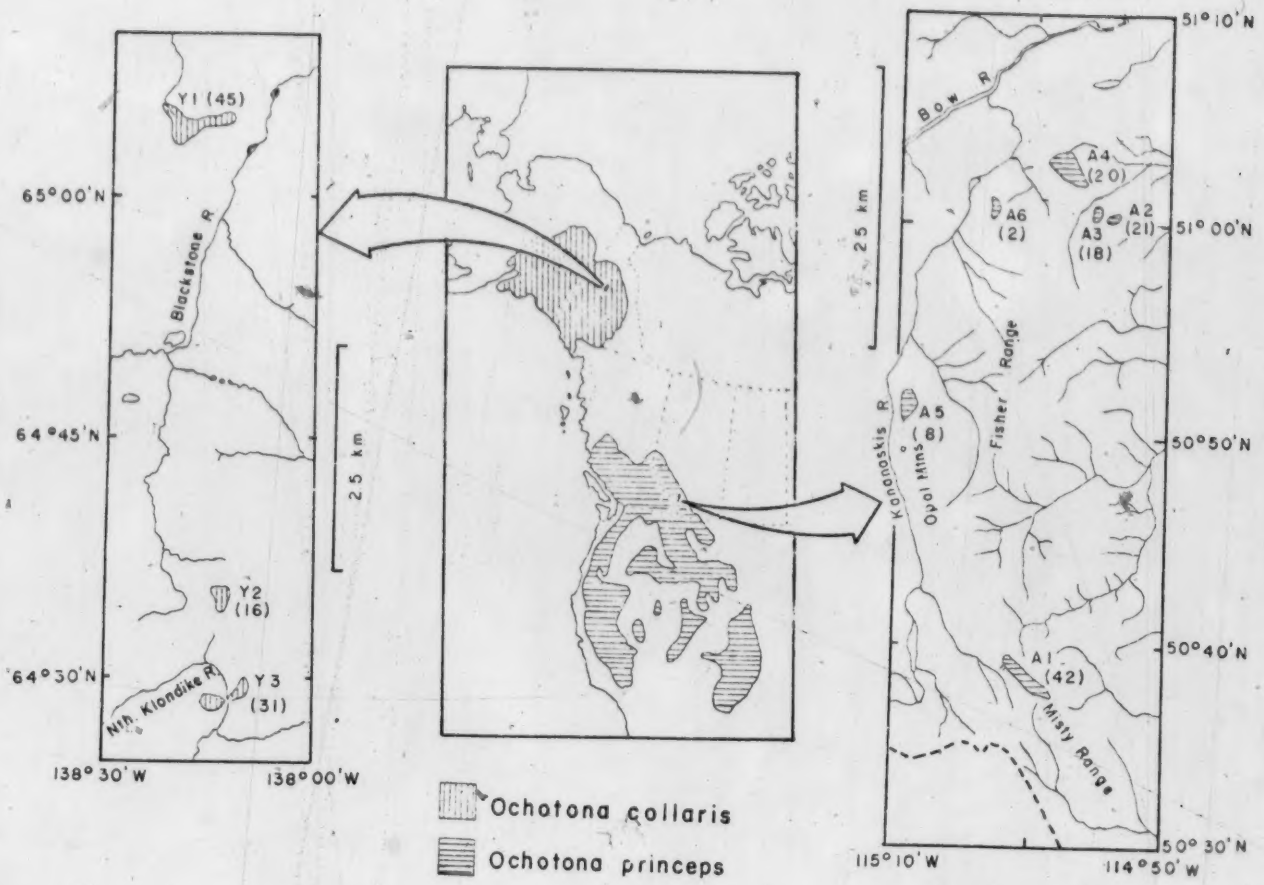
CHAPTER I

INTRODUCTION

Helminth communities are usually difficult to delimit because more than one host species must be considered as part of the host-helminth system. Helminth communities of pikas (*Ochotona* species) in North America are an exception because no helminths that mature in pikas have been reported in other hosts, and the two species of *Ochotona* in North America are allopatric (see Figure 1). Thus, unlike other helminth communities (e.g., Kisielewska, 1970a; Bush, 1973), none of the helminths inhabiting pikas can be regarded as an immigrant or accidental species.

The major objective of this study was to gather information on the dynamics of two pika-helminth community systems: (1) the helminths of *O. collaris* from northern Yukon Territory, and (2) the helminths of *O. princeps* from southwestern Alberta. Aspects of population and community structure were examined at the host-species, host-population, and host-individual levels. At the broadest, or host-species level, the geographical distribution of hosts and helminths is reviewed. A more restricted level, the host-population level, is analyzed to answer such questions as when and how do pikas acquire their helminths. The most

Figure 1. Map of North American distribution of pikas, showing study areas. Sample sizes from each site are shown in parentheses. The distribution map is based on Hall and Kelson (1959).


Y1 (45)
65°00'N
Blackstone R.
64°45'N
25 km
Y2 (16)
64°30'N
Nth. Klondike R.
Y3 (31)
138°30'W
138°00'W
Ochotona collaris
Ochotona princeps
51°10'N
Bow R.
A4 (20)
A6 (2)
A2 (21)
A3 (18)
51°00'N
25 km
Kananaskis R.
Opal Mtns.
A5 (8)
Fisher Range
50°50'N
50°40'N
A1 (42)
Misty Range
50°30'N
115°10'W
114°50'W

restricted, or host-individual level, is examined in terms of interactions between species of helminths.

Simpson (1945) states that "animals cannot be discussed or treated in a scientific way until some taxonomy has been achieved." This is particularly appropriate for studies of community dynamics, so taxonomic problems were examined prior to the ecological study. The solution of these problems subsequently became a major objective in itself.

CHAPTER II

MATERIALS AND METHODS

Necropsies were performed on 111 *O. princeps* individuals from Alberta, and 92 *O. collaris* individuals from the Yukon Territory. All the *O. collaris*, and 102 *O. princeps* were collected by shooting. Pikas were shot in Alberta from May to August, 1971, and in the Yukon Territory from June to August, 1972. Seven *O. princeps* were trapped in November, 1971, one in December, 1971, and one in April, 1972, using weasel snap-traps baited with lettuce. With the exception of the April-caught pika, carcasses of those caught in traps were frozen, and necropsied later in the laboratory. The April-caught pika was necropsied fresh within 18 hrs. of death.

Within five minutes of death, the pika's abdomen was opened, and the gastro-intestinal tract tied off into sections with cotton thread, to prevent post-mortem migration of helminths. All the pikas which were collected by shooting were examined within six hrs. of death.

Conventional methods were used in collection of gastro-intestinal helminths. Nematodes were fixed in 5% glycerine in 70% ethanol; cestodes were relaxed in cold water and either fixed in AFA, or stained in Blachin's lactic acid

carmine stain.

Conventional methods of preparation and staining of parasites were employed. Nematodes were cleared in lactophenol creosote. Measurements were made with the aid of an ocular micrometer, or camera lucida and measuring wheel. Sample sizes for measured pinworms are shown in Appendix I. The anterior ends of some nematodes were mounted *en face* in glycerine jelly, using a modified technique of Anderson (1958). The modification was suggested by A.O. Bush (pers. comm.), and entailed mounting the end section face down in a drop of warm glycerine jelly on a circular coverslip. The anterior end could be brought very close to the coverslip, or even in contact with it, and was easily positioned with a fine probe. When correctly positioned, the coverglass was quickly cooled to harden the glycerine jelly. When it was set, a warm square coverglass was placed on top of the glycerine jelly without disturbing the position of the tissue section, and allowed to cool. The resulting sandwich was then mounted on a glass slide, round coverslip up, with Canada balsam.

Fixed cestodes were stained in either Harris' haemotoxylin or Semichon's acetocarmine.

Juvenile pikas were aged based on their weight (Millar and Tapper, 1973). Confirmation that some of the heavier juveniles were not adults was by sectioning the lower jaw (Millar and Zwickel, 1972a).

In determining relationships of individuals at the

species level, decisions were mostly arbitrary, and were based on morphology and geographic distribution. Specimens available for study and those used for descriptions in the literature, were usually from widely scattered populations, such that distributional data were sketchy. In most cases, if morphological variation within a population was exceeded by differences between populations, individuals were classified as two species. In some cases where there was insufficient morphological evidence, I have recognized two species based on geographical distribution, where there may be only one (e.g., *Eugenuris schumakovitschi* and *E. talkeetnaeuris*). Members of congeneric species were found to be sympatric in only one genus (*Cephaluris*), and I have used a more biological definition of species in making decisions between individuals inhabiting hosts of a single population for that case.

CHAPTER III

STUDY AREAS

Specimens of *Ochotona princeps* were collected for this study from the eastern slopes of the Rocky Mountains of southwestern Alberta, and of *O. collaris* from the Ogilvie Mountains of central Yukon Territory (Figure 1).

Alberta

Pikas were collected from several locations in Alberta, all in the mountains and foothills to the east of the Kananaskis River.

1. Highwood Pass (Site A1)

Specific collection sites, ranging in elevation from 2000 to 2500 m., were on the west sides of Mt. Rae, Mt. Arethusa and Storm Mountain of the Misty Range, and at the southern tip of the Opal Range on the south slope of Mt. Elpoca. Peaks in these Ranges reach over 3400 m. elevation. The mean annual precipitation for the period 1965 to 1969 was 92.58 cm, 29.97 cm as rain and 62.61 as snow (Watershed Research Branch, from Trottier, 1972). This high precipitation in winter is a maritime distribution, more characteristic of the central ranges of the Rocky Mountains, whereas

the eastern ranges typically receive a continental distribution. The other study areas of Alberta fall into the latter category. For a detailed description of the alpine vegetation in this region, consult Trottier (1972).

2. Cox Hill Summit (Site A2)

The major collection site in the foothills region was a dome-shaped mountain, Cox Hill (51°00'N, 114°54'W). Two locations on this hill were sampled, which I call the Summit, and the Northwest Ridge. The latter is considered separately because it supports a different pika helminth fauna.

Talus slides on the Summit range in elevation from 1900 to 2100 m., and face northwest. It was an open, exposed, dry site. Vegetation surrounding the talus was dominated by grasses and *Zygadenus elegans*. *Dryas octopetala*, *Antennaria* sp. and *Potentilla fruticosa* were also abundant. The lower reaches of this site were among young *Pinus contorta* forest, the floor of which was dry, and covered with dead needles. Other common plants here were *Hedysarum mackenzii*, *Ribes* sp., *Juniperus communis*, grasses, and *Arctostaphylos uva-ursi*.

3. Cox Hill Northwest Ridge (Site A3)

This area is only 1.5 km. west of the slides at the Summit. Elevation of the collection sites ranges from 1700 to 1900 m. Slides were nestled amongst *Picea englemannii*/ *Pinus contorta* forest, and face north. The forest floor

was fairly dry, shaded, and covered with dead pine needles, particularly at the base of the slides. Vegetation around the talus was dominated by *Cladonia* sp., *Arctostaphylos uva-ursi*, grasses, *Ribes* sp., and *Dryas octopetala*.

4. Miscellaneous (Sites A4, A5, and A6)

Pikas from these areas were not included in the comparisons between locations, and since collections were scattered over a wide variety of habitat types, I shall not describe them in detail. Locations and sample sizes are shown in Figure 1.

Yukon Territory

The Ogilvie Mountains are north of the Tintina Trench in central Yukon. The northern part of this Range consists of limestone, and the southern part of sandstones and volcanic rocks. Pikas were collected from three sites.

1. North (Site Y1)

Pikas were collected within 2 km. of the Dempster Highway from mile 83 to mile 100 (65°00'N, 138°15'W), at elevations ranging from 920 to 1380 m. (Figure 1). The dome-shaped mountains of this area reach elevations of about 1700 m. from valleys of 900 m. Pikas were found predominantly around the base of these mountains, where vegetation was most abundant, but many were also found higher, as much of the surface was covered by talus and scattered vegetation.

Slopes were generally open, dry, and supported a vegetation dominated by *Dryas integrifolia*, *D. octopetala*, grasses, and *Cladonia* sp.. Open *Picea glauca* forests were found in some of the lower sites, with willow shrubs, *Betula nana*, and a moist mossy floor. Pika haypiles in late summer consisted mostly of *Dryas* leaves and flower heads, grasses, *Arctostaphylos uva-ursi* and *A. rubra*.

2. Central (Site Y2)

The Dempster Highway crosses the North Fork Pass, which marks the divide of the Yukon River drainage to the south, and the Mackenzie River drainage to the north. Pikas were collected on Sheep Mountain (64°35'N, 138°12'W), to the east of the pass. The entire area is well above timberline (1000 m.); collection sites range from 1500 to 1900 m. elevation. Much of the vegetation was dominated by *Dryas* spp., and grasses, with patches of *Cassiope tetragona*. Also present in moist areas with running water were *Salix* spp., *Sedum rosea* and *Oxyria digyna*. Haypiles consisted mostly of *Dryas* leaves and flower heads, and grasses.

3. South (Site Y3)

At mile 43, the Dempster Highway crosses the North Klondike River (64°28'N, 138°10'W). Mountains on both sides of the river reach elevations of about 1900 m. Pikas were collected from these mountains at elevations ranging from 1100 to 1800 m. Vegetation was generally similar to

Site Y2, dominated by *Dryas octopetala* and grasses, with patches of *Cassiope tetragona*. Many slides encroached upon moist meadows with flowing streams. Here the vegetation was dominated by sedges and grasses, with *D. octopetala*, *Salix* spp., and *Epilobium latifolium*. Haypiles contained *Dryas*, grasses, *Oxyria*, *Equisetum*, *Potentilla*, and *Arctostaphylos*.

CHAPTER IV

HOST NATURAL HISTORY

As far as is known, both *Ochotona princeps* and *O. collaris* have similar life histories in terms of habitat requirements, seasonal and daily activities, reproduction, and social structure (Broadbooks, 1965). Dwellings are located in the interstices of rocks, but pikas usually must leave the talus to feed. They eat a great variety of grasses and forbs depending upon availability (Broadbooks, 1965; Rausch, 1962; Millar and Zwickel, 1972b). Most foraging is carried out within 20 m. of the talus, but longer trips have been observed (personal observations; Smith, 1974b). Because of the nature of their habitat, pikas are usually located in scattered and discrete populations, which is of great significance to their dispersal (Tapper, 1973; Smith, 1974a).

Weather conditions modify the daily activities of pikas, but they are essentially diurnal. On fine sunny days, observable activity (including feeding) is primarily in the morning and late afternoon, with less around midday, while on cloudy days, activity is at a peak around midday (Sharp, 1973). Presumably they are avoiding heat stress on hot days.

Millar (1972) studied reproduction in *O. princeps* of

southwestern Alberta. Two litters, each of 2-3 young per female were born each year. The mean date of conception for the first litter was May 9th and for the second litter June 12th. The gestation period is 30 days (Severaid, 1950), and weaning occurs 3-4 weeks after birth (Severaid, 1950; Millar, 1972).

Soon after weaning, juveniles either disperse or wedge between territories on their home slide (Tapper, 1973). Dispersing juveniles are usually unsuccessful in establishing themselves on occupied habitat. This further isolates the populations into discrete "islands".

The abundance of pikas on a rockslide is quite stable and regulated by territoriality (Tapper, 1973). Male home ranges overlap considerably with those of females until after the period of breeding. They then shrink to become individual home ranges, which are defended more rigorously with the onset of the haying season in July (Sharp, 1973). Haying, the storage of vegetation in the rocks, continues at least into September (personal observation).

Pikas, like other lagomorphs, produce two kinds of faeces, soft and hard. Severaid (1955) observed captive *O. princeps* ingesting soft faeces, and Tyndale-Biscoe (1959) found evidence of reingested soft faeces in the stomachs of wild *O. roylei* caught at night. Haga (1960) claimed that Japanese pikas, *O. hyperborea yesoensis*, produce soft faeces at night only although he produced no evidence. In contrast to the findings of Tyndale-Biscoe and Haga, pikas

in Colorado (*O. princeps*) were found to produce soft faeces during the day (Johnson, 1967), as in wild rabbits and hares.

Individuals of both species of pikas in the present study produced soft faeces during the day. More individuals of *O. princeps* produced soft faeces in the morning (0700-0900 hrs.: 58%) and mid-afternoon (1400-1600: 69%) than during in-between times (34%), thus roughly corresponding to feeding periods. No such trend was present with *O. collaris*, perhaps because the feeding period is not as distinctly bimodal, due to extended summer daylight in high latitudes.

CHAPTER V

TAXONOMY

The purpose of this section is to clarify the status of the named taxa of helminths whose members mature in pikas, to summarize host and geographic distribution, and to assist in the identification of these helminths. Table 1 lists names of taxa of the two Nearctic helminth communities as defined in the broadest context, the host species level. The communities comprise seven species in *O. princeps*, and five species in *O. collaris*. All these species, and other species in the six genera represented, are known exclusively from pikas.

The taxa of each genus are treated in some detail below, with keys, discussions of features thought to be of diagnostic value, and data on distribution.

Schizorchis Hansen 1948

Schizorchis Hansen 1948: 754. TYPE SPECIES:- *S. ochotonae* Hansen 1948 (by monotypy).

Although five species have been ascribed to this genus, Rausch and Ohbayashi (1974) have shown that *S. esarsi* Lovekar, Seth and Deshmukh 1972 from the mouse *Mus musculus* in India, does not belong to this genus and is near *Atriotaenia*

Table 1. List of names of the two helminth communities of pikas

Helminth taxon	Host Species	
	Ochotona princeps	*Ochotona collaris*
Phylum Platyhelminthes		
Class Cestoda		
Fam. Anoplocephalidae	*Schizorchis caballeroi*	*Schizorchis caballeroi*
Phylum Nematoda		
Superfam. Oxyuroidea		
Fam. Oxyuridae	*Cephaluris alaskensis*	*Cephaluris alaskensis*
	Cephaluris coloradensis	*Cephaluris coloradensis*
	Eugenuris species A	*Eugenuris talkeetnaeuris*
	Labiostomum coloradensis	*Labiostomum rauschi*
Superfam. Trichostrongyloidea		
Fam. Heligmosomidae	*Murielus harpespiculus*	
Fam. Trichostrongylidae	*Graphidiella ochotonae*	

Sandground 1926. The four remaining species in this genus are distinguished by the following key.

Key to the Species of *Schizorchis* Hansen

1A. Outer egg shell covered with tubercles or spines ---------- *S. altaica* Gvozdev 1951

1B. Outer egg shell smooth ---------- (2)

2A. Testes not separated into two distinct lateral bands; cirrus sac 286-428 micrometres long ---------- *S. yamashitai* Rausch 1963

2B. Testes separated into two distinct lateral bands; cirrus sac longer than 450 micrometres ---------- (3)

3A. Strobila wedge-shaped, up to 5 mm wide; testes and uterus not reaching ventral longitudinal excretory canals; ovary slightly more anteriad than level of testes ---------- *S. ochotonae* Hansen 1948

3B. Strobila slender, up to 3 mm wide; testes and uterus reaching ventral longitudinal excretory canals on both sides; ovary at same level as testes ---------- *S. caballeroi* Rausch 1960

1. Notes on Diagnosis

In distinguishing Nearctic species, Rausch (1960) stated that the genital atrium was more posterior in specimens of *S. caballeroi* than of *S. ochotonae*, but my observations do not confirm this. He also reported that the uterus of *S. caballeroi* specimens did not extend laterad to the excretory canals, but in many of the specimens which I examined, the uterus does extend laterad. I found the cirrus to be

spined on some specimens of *S. caballeroi* in *O. collaris*. The spines were very fragile, and apparently easily lost. A spined cirrus has been reported previously on specimens of this genus, only for *S. altaica* (Gvozdev, 1951). My observations suggest that such spines may have been overlooked in specimens of other species, and should not be used as a diagnostic character.

Palaearctic species are *S. altaica* Gvozdev 1951, and *S. yamashitai* Rausch 1963. *Schizorchis altaica* was redescribed soon after being described (Spasskii and Ryzhikov, 1951). The original description was of a worm 150 mm long, whereas worms measured for the redescription were 60-70 mm long. Although Gvozdev appears to favour the redescription (Gvozdev et al., 1970), Rausch (1960, 1963a), and Rausch and Ohbayashi (1974) suggest that these may be two species. Rausch and Ohbayashi (1974) identified two specimens from *O. roylei* of Nepal as *S.* cf *altaica* because they most resembled specimens described as *S. altaica* by Spasskii and Ryzhikov. Rausch and Ohbayashi (1974) did not characterize the outer egg shell, which seems to offer the only characteristic distinguishing between members of *S. altaica* and other members of the genus. The material described by Rausch and Ohbayashi seems to be indistinguishable from specimens of *S. caballeroi*. Accordingly, members of *S.* cf *altaica* may be conspecific with members of *S. caballeroi*, and if differences in egg shells are not diagnostic, then these may be conspecific with members of *S. altaica*.

The species *S. yamashitai* is clearly recognizable by characteristics presented in the key.

2. Host Records and Geographic Distribution

In the Nearctic, *S. ochotonae* is known only from *O. princeps*, in Colorado (Hansen, 1948 - type area; Leiby, 1961a), California (Voge, 1955; Severaid, 1955), Wyoming (Rausch, 1960), Utah (Warnock, 1962; Grundmann and Lombardi, 1976), Nevada (Grundmann and Lombardi, 1976), Idaho (Seesee, 1973), Montana (Barrett and Worley, 1970), and Alberta (Lubinsky, 1957). The species *S. caballeroi* has been reported from both Nearctic species of pikas: *O. princeps* in Oregon (Rausch and Ohbayashi, 1974), and Alberta (this study); and *O. collaris* in Alaska (Rausch, 1960 - type area) and Yukon Territory (this study). The two Nearctic species of *Schizorchis* are not easily distinguishable, and I suspect that many investigators have assumed specimens obtained from specimens of *O. princeps* to be *S. ochotonae*, merely because *S. caballeroi* had not been reported in *O. princeps*.

A summary of the known distribution of the Palaearctic species is presented in Table 2.

Murielus Dikmans 1939

Murielus Dikmans 1939: 2. TYPE SPECIES:- *M. harpe-spiculus* Dikmans 1939 (by monotypy).

Three species (one Holarctic and two Palaearctic) are included in this genus, members of which are distinguished

Table 2. Host records and data on geographical distribution of the Palaearctic species of *Schizorchis* Hansen

Host	*S. altaïca*	*S.* cf *altaica*	*S. yamashitai*
Ochotona roylei		x[5]	
O. rutila	x[1]		
O. alpina	x[2]	x[6]	
O. hyperborea	x[3]		x[7]
O. macrotis	x[4]		

1-7 Localities: 1. Tyan Shan (Tokobaev, 1960); 2. Kazakhstan (Gvozdev, 1951 - type area); 3. Yakutia (Gubanov, 1964), Taymyr (Mustafaev, 1968); 4. Tyan Shan (Gvozdev, 1964; Tokobaev, 1960); 5. Nepal (Rausch and Ohbayashi, 1974); 6. Pribaikal (Spasskii and Ryzhikov, 1951); 7. Japan (Rausch, 1963a - type area; this study).

by the key below.

Key to the Species of *Murielus* Dikmans

1A. Spicules 480 micrometres long, united at tips, but without barbed head ---- ---------- *M. abei* Durette-Desset 1974

1B. Spicules 700-900 micrometres long, united at tips in a barbed head (Figure 2a) ---------- (2)

2A. Externolateral bursal rays in males much smaller than other laterals; most medial of the three dorsal rays with a minute appendage (Figure 2b); synlophe of both sexes with only one pair of robust lateral crêtes (Figure 2c) ---------- *M. harpespiculus* Dikmans 1939

2B. Externolateral bursal rays almost as stout as other laterals; no appendage on most medial dorsal ray; synlophe with two pairs of more robust lateral crêtes (Figure 2d) ---------- ---------- *M. tjanshaniensis* Gvozdev 1962

1. Notes on Diagnosis

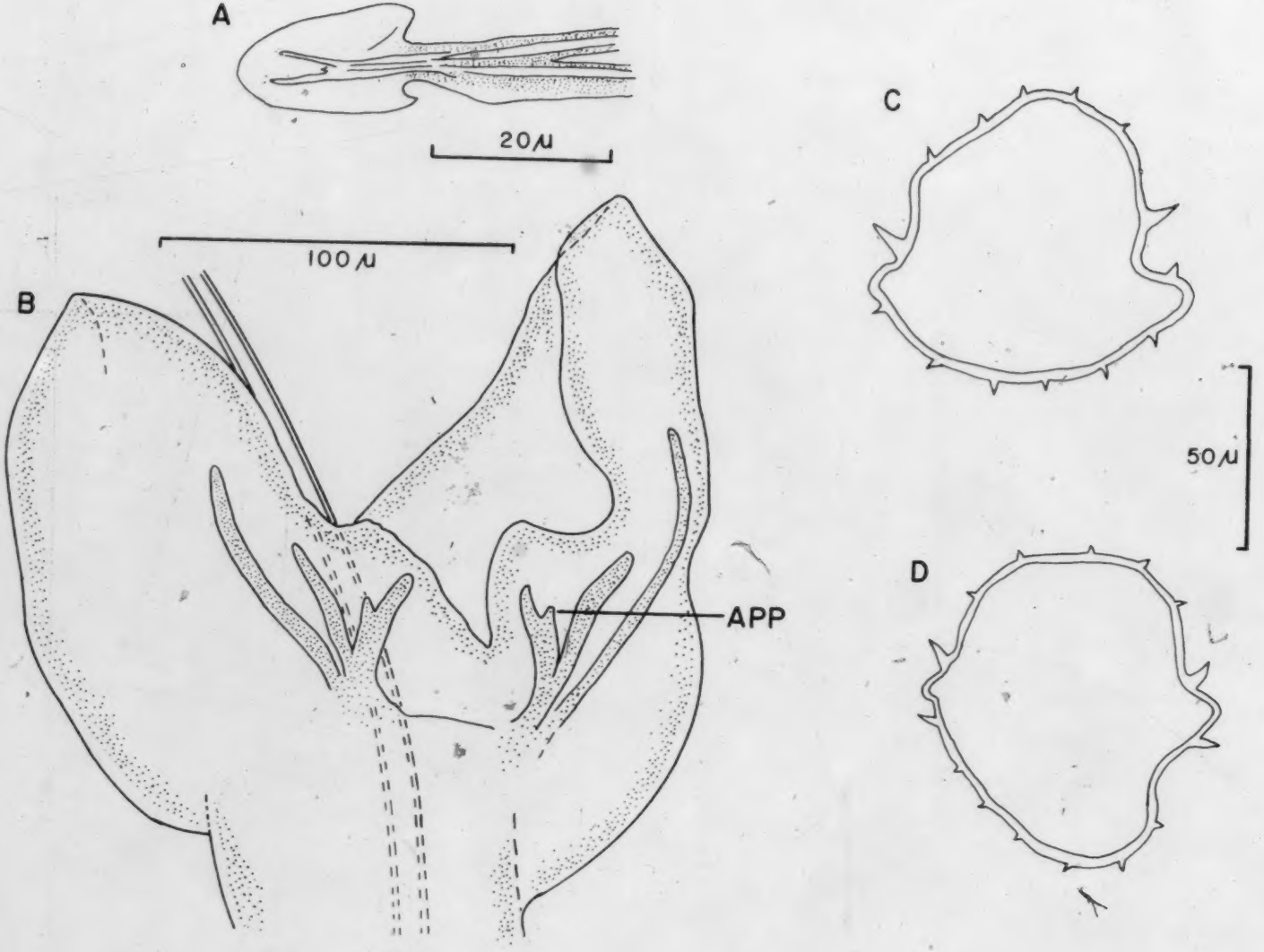
Males of *M. tjanshaniensis* were distinguished from those of *M. harpespiculus* by Gvozdev et al. (1970), by the arrangement of the dorsal group of bursal rays. Although the differences given sound clear, members of both species possess three pairs of rays in the dorsal group. Specimens of *M. tjanshaniensis* are described as having the inner two pairs joined, while those of *M. harpespiculus* are described as having rays separated for their entire lengths. However, close study indicates that these characteristics vary appreciably, and the differences are not diagnostic. Also, differences in tail shape between females of the two species

Figure 2. a) spicule tip of *Murielus harpespiculus*

b) dorsal bursal rays of *M. harpespiculus* (APP - appendage)

c) synlophe of *M. harpespiculus*

c) synlophe of *M. tjanshaniensis*


A
20 μ
100 μ
B
APP
C
50 μ
D

are not diagnostic because of intraspecific variation.

Durette-Desset (1974) distinguishes members of *M. abei* from those of the other two species by the following characteristics, which I find unreliable:

1. Three pairs of dorsal rays are separate from each other in specimens of *M. abei*. I have found this to be characteristic of some specimens of *M. harpespiculus*.

2. Specimens of *M. abei* are distinguished from those of *M. harpespiculus* by the equal lengths of rays 10 and 11 in *M. abei*. Although I was unable to satisfactorily determine to which dorsal rays these numbers refer, all the dorsal rays in her figure 2H are of different lengths. In another figure of the bursa (2I), two of the dorsal rays are of equal length, but these correspond with the two that are equal in specimens of *M. harpespiculus* (see Durette-Desset's figure 1D, or Dikmans' (1939) figure 2E).

3. She distinguishes *M. abei* from *M. tjanshaniensis* by the relative sizes of the lateral rays. The posterolateral are equal to the mediolateral in specimens of *M. abei*, but this is also true for specimens of *M. tjanshaniensis* (Gvozdev et al., 1970).

4. She distinguishes among the three species by the number of crêtes: 14 for *M. harpespiculus*, 15 for *M. tjanshaniensis*, and 16 for *M. abei*. This characteristic varies: I have found from 14 to 16 crêtes in specimens of *M. harpespiculus*, and from 15 to 18 in specimens of *M. tjanshaniensis*. The synlophe of *M. abei* (figure 2C, Durette-Desset, 1974)

appears to be identical to that of *M. tjanshaniensis*, members of both species having two pairs of enlarged lateral crêtes, and thus differing from members of *M. harpespiculus*.

Host records and geographic distribution are presented in Table 3.

Graphidiella Olsen 1948

Graphidiella Olsen 1948: 749. TYPE SPECIES:- *G. ochotonae* Olsen 1948 (by monotypy).

Two species, the Nearctic *G. ochotonae*, and the Palaearctic *G. olsoni* Gvozdev 1966, are included in this genus, members being distinguished by the following key.

Key to the Species of *Graphidiella* Olsen

1A. Spicules 660-770 micrometres long; eggs 180 micrometres long; body length of females 17.7-23.2 mm, and of males 11.1-17.4 mm ---------- *G. ochotonae* Olsen 1948

1B. Spicules 400-550 micrometres long; eggs 165 micrometres long; body length in females 12-13.5 mm, and of males 8.6-9.8 mm ---------- *G. olsoni* Gvozdev 1966

1. Notes on Diagnosis

Apparently, Olsen (1948) misinterpreted the structure of the ovejector of female *G. ochotonae*. He stated that these structures were triple-bulbed. However, Alberta and Idaho females have single-bulbed ovejectors, and Seesee (1973) reported that paratypes of this species were similarly characterized. Female *G. olsoni* Gvozdev also have single-

Table 3. Host records and data on geographical distribution of the species of *Murielus* Dikmans

Host	*M. harpespiculus*	*M. tjanshaniensis*	*M. abei*
Ochotona princeps	X[1]		
O. roylei			X[6]
O. rutila		X[3]	
O. hyperborea	X[2]		
O. macrotis		X[4]	
O. daurica		X[5]	

1-6) Localities: 1. Wyoming (Dikmans, 1939 - type area), Montana (Barrett and Worley, 1970), Idaho (Seesee, 1973), Colorado (Leiby, 1961a), Utah (Warnock, 1962; Grundmann and Lombardi, 1976), Nevada (Grundmann and Lombardi, 1976), California (Severaid, 1955); 2. Taymyr (Mustafaev, 1968); 3. Altai Mountains (Gvozdev, 1962 - type area); 4. Tyan Shan (Gvozdev, 1964); 5. Tuva (Sulimov and Obukhov, 1974); 6. Nepal (Durette-Desset, 1974 - type area).

bulbed ovejectors, so this feature cannot be used to distinguish between the two species. Gvozdev (1966) differentiated between males of the two species by the shape of the dorsal ray. However, intraspecific variation is too great for this character to be of use.

2. Host Records and Geographic Distribution

The Nearctic *G. ochotonae* is known only from *O. princeps* in Colorado (Olsen, 1948 - type area), Idaho (Seesee, 1973), Montana (Barrett and Worley, 1970), and Alberta (this study). Martin (1943) reported "stomach worms" from pikas in Wyoming, which are almost certainly *G. ochotonae*. The Palaearctic *G. olsoni* is known from specimens of *O. alpina* from the Sayan Mountains of eastern Siberia (Gvozdev, 1966 - type area) and specimens of *O. daurica* from Tuva (Sulimov and Obukhov, 1974).

Cephaluris Akhtar 1947

Cephaluris Akhtar 1947: 104. TYPE SPECIES:- *C. ochotonae* Akhtar 1947 (by monotypy).

This genus includes six species, arrayed into two groups. The taxa are distinguished from one another in the following key.

Key of the Groups and Species of *Cephaluris* Akhtar

1A. Blunt, rugged teeth on ventral precloacal ridge; subcuticular longitudinal bands or bosses in caudal alae; greatly expanded cushion-like posterior papilla ---------- Group 1..(2)

1B. Fine, thin teeth on ventral ridge; longitudinal bands or bosses absent; relatively deflated cushion-like posterior papilla ---------- Group 2..(4)

2A. Discontinuous bosses in caudal alae ---------- *C. hashmi* Akhtar 1956

2B. Continuous longitudinal bands in caudal alae ---------- (3)

3A. Cloaca closer than 700 micrometres from tail tip; nerve ring closer than 195 micrometres from anterior end; buccal cavity shallower than 35 micrometres; Nearctic distribution -------- ---------- *C. alaskensis* Akhtar 1958

3B. Cloaca further than 700 from tail tip; nerve ring further than 195 from anterior end; buccal cavity deeper than 35; Palaearctic distribution --- ---------- *C. andrejevi* Shul'ts 1948

4A. Cloacal papillae asymmetrical ------- ---------- *C. chabaudi* Inglis 1959

4B. Cloacal papillae symmetrical ---------- (5)

5A. Body shorter than 8 mm, and narrower than 400 micrometres; Nearctic distribution ---------- *C. coloradensis* Olsen 1949

5B. Body longer than 8 mm, and wider than 400 micrometres; Palaearctic distribution ---------- *C. ochotonae* Akhtar 1947

1. Notes on Synonymy

Hobbs (in press) showed that the name *C. uakhanica* Erhardova-Kotrla and Daniel 1970 is a junior synonym of *C. ochotonae*, and that *C. collaris* Akhtar 1958 is a junior synonym of *C. coloradensis*.

2. Notes on Diagnosis

Within Group 1, members of *C. alaskensis* and *C. andrejevi* are so similar to one another that they may be conspecific. The males differed slightly in measurements of tail length, position of the nerve ring, and depth of the buccal cavity. It was impossible to compare females of these species, since the North American collections were from mixed infections of *C. alaskensis* and *C. coloradensis*, the females of which were indistinguishable. Although *C. andrejevi* and *C. alaskensis* are very close morphologically, I consider it safer at the present time to regard them as separate species. Less closely related is *C. hashmi*.

A similar situation exists with *C. ochotonae* and *C. coloradensis* in Group 2. Males of the latter species differ only in body length and width from males of *C. ochotonae*. Females of *C. ochotonae* possess a vulval flap, whereas no North American specimens had one. Members of *C. chabaudi* are easily distinguishable from those of the other two species in this group.

3. Host Records and Geographic Distribution

In the Nearctic, Group 1 is represented by *C. alaskensis*, specimens of which have been collected from *O. princeps* specimens in Alberta and Colorado (Hobbs loc. cit.), and from *O. collaris* specimens in Alaska (Akhtar, 1958 - type area) and the Yukon (Hobbs loc. cit.). Group 2 is represented in the Nearctic by *C. coloradensis*, specimens of which

have been collected from specimens of *O. princeps* in Colorado (Olsen, 1949 - type area; Leiby, 1961a; Hobbs loc. cit.), Utah (Warnock, 1962; Grundmann and Lombardi, 1976), California (Severaid, 1955; Voge, 1956), Nevada (Grundmann and Lombardi, 1956), Montana (Barrett and Worley, 1970), Idaho (Seesee, 1973), and Alberta (Hobbs loc. cit.); and from *O. collaris* specimens in the Yukon (Hobbs loc.cit.) and Alaska (Akhtar, 1958). Some of these reports may not be entirely accurate however, since I found specimens of *C. alaskensis* to be more common than *C. coloradensis* in all locations studied; even some of the syntypes for *C. coloradensis* were *C. alaskensis* (Hobbs loc. cit.).

Distribution of Palaearctic species of *Cephaluris* is presented in Table 4.

Eugenuris Shul'ts 1948

Eugenuris Shul'ts 1948: 173. TYPE SPECIES:- *E. schumakovitschi* Shul'ts 1948 (by monotypy). Akhtar 1956b: 137. Barus et al. 1972: 14. Skryabin et al. 1960: 259; 1967: 198. Grundmann and Lombardi 1976: 45.

Dermatoxys Dubinin and Dubinina 1951: 113, (not Schneider 1866). Tokobaev 1960: 240. Erhardova-Kotrla and Daniel 1970: 208.

Pikaeuris Akhtar 1953: 84. TYPE SPECIES:- *P. pikaeuris* Akhtar 1953 (by absolute tautonomy and monotypy). Akhtar 1956b: 133. Yamaguti 1961: 550. Skryabin et al. 1960: 233; 1967: 198.

Table 4. Host records and data on geographical distribution of the Palaearctic species of *Cephaluris* Akhtar

Host	*Cephaluris*			
	Group 1		Group 2	
	C. andrejevi - *C. hashmi*		*C. ochotonae* - *C. chabaudi*	
Ochotona rufescens	x[1]	x[8]	x[9]	x[12]
O. roylei			x[10]	
O. rutila	x[2]		x[11]	
O. alpina	x[3]			
O. hyperborea	x[4]			
O. daurica	x[5]			
O. macrotis	x[6]			
O. pallasi	x[7]			

1-12 Localities: 1. Turkmenia (Babaev, 1967); 2. Kirghizii (Tokobaev, 1960); Kazakhstan (this study); 3. northern Altai (Shul'ts, 1948 - type area), Pribaikal (Spasskii and Ryzhikov, 1951), Zabaikal (Dubinin and Dubinina, 1951), and southern Altai (Gvozdev, 1956); 4. lower Lena region (Kapitonov, 1961), Yakutia (Gubanov, 1964), and Taymyr (Mustafaev, 1968); 5. Zabaikal (Dubinin and Dubinina, 1951), eastern Mongolia (Meszaros, 1974); 6. Kirghizii (Tokobaev, 1960), and Tyan Shan (Gvozdev, 1964); 7. Kazakhstan (Gvozdev, 1956); 8. Pakistan (Akhtar, 1956a - type area); 9. Afghanistan (Akhtar, 1947 - type area; Barus et al., 1972); 10. Hindu Kush (Erhardova-Kotrla and Daniel, 1970); 11. Kazakhstan (new record; originally determined as *C. andrejevi*); 12. Iran (Inglis, 1959 - type area), Turkmenia (Babaev, 1967).

Labiostomum Inglis 1959: 186 (not Akhtar, 1941).

1. Notes on Synonymy

Although members of *Eugenuris* share with those of *Dermatoxys* a pre-cloacal comb, the two groups are readily distinguished by differences in structure of the anterior end (mouth, number and shape of lips) (Barus et al., 1972). Also the pre-cloacal comb of the two groups is different in detail, and furthermore, the comb of *Eugenuris* is more like that of the other pika pinworms (*Labiostomum*, *Cephaluris* and *Fastigiuris* Babaev, 1966), than like that of *Dermatoxys*. The ventral ridge in pika pinworms is a narrow, laterally compressed ridge, while in members of *Dermatoxys* found in other groups of lagomorphs, the ridge is a line of transverse teeth. Thus, *Eugenuris* and *Dermatoxys* are not congeneric.

Akhtar (1956b) reported that members of *P. pikaeuris* Akhtar 1953 differed only slightly from members of *E. schumakovitschi*, and that these two species were congeneric. Thus the name *Pikaeuris* is a junior subjective synonym of *Eugenuris*, Yamaguti (1961) and Skryabin et al. (1960, 1967) not withstanding.

Although members of *Eugenuris* differ from those of *Labiostomum* in cephalic structure (Barus et al., 1972), the two groups were considered to be congeneric by Inglis (1959), who had not seen specimens of *Eugenuris*. Evidently, he thought the differences were artefacts of fixation. In addi-

tion to differences in cephalic structures, females of *Labiostomum* have a constriction just anterior to the tip of the tail, whereas females of *Eugenuris* have a gradually tapered tail. Hence, these two groups of species are clearly distinct.

2. The Species

This genus includes five formally named species and a fifth, designated here as *Eugenuris* species A. The Nearctic representatives are distinguished from one another in the following key.

Key to the Nearctic Species of *Eugenuris* Shul'ts

1A. Eggs operculated at each pole; two uteri empty separately into ovejector anteriad to vulva ---------- *E. utahensis* Grundmann and Lombardi 1976

1B. Eggs operculated at one pole; single uterus formed by fusion of two uteri posteriad to anus empties into the ovejector at the level of the vulva ---------- (2)

2A. Cloacal papillae of males as follows: large "b", small "d", "g" broad or absent (Figure 3a); buccal cavity depth in females 62 micrometres, in males 51 *E. talkeetnaeuris* Akhtar 1956

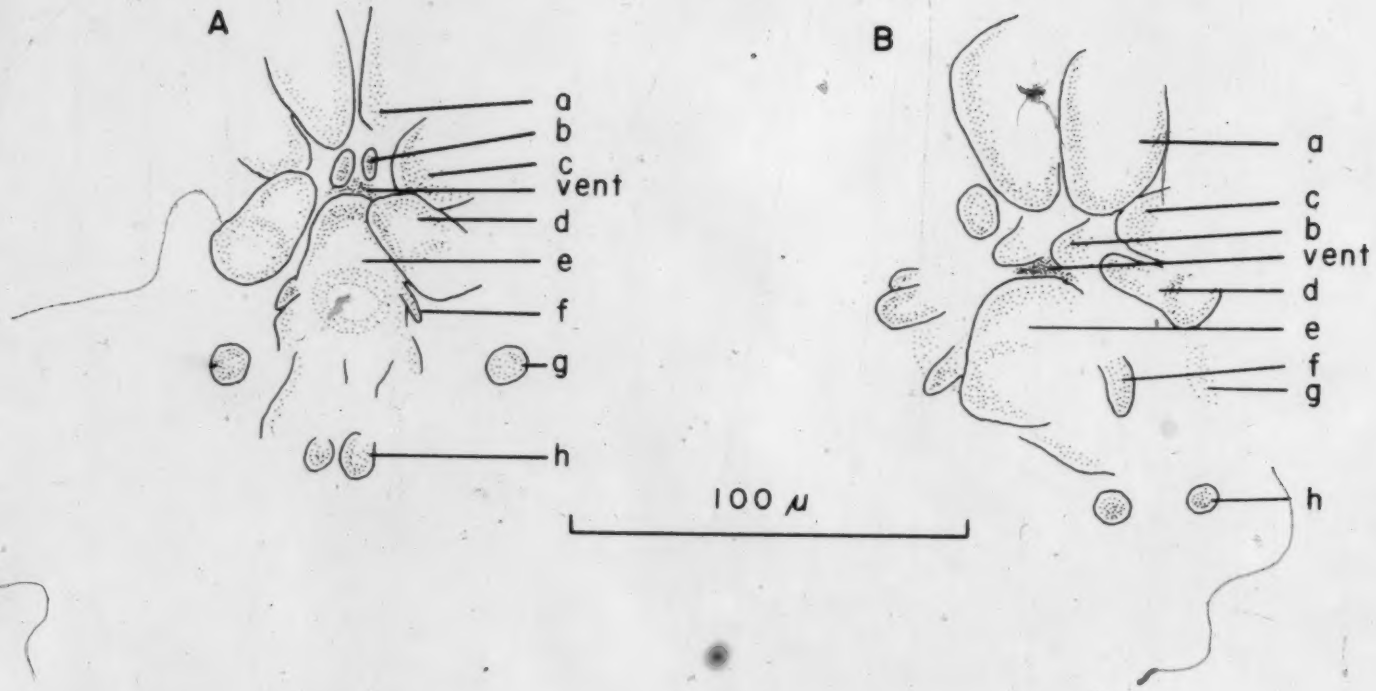
2B. Cloacal papillae as follows: small "b", large "d", compact "g" (Figure 3b); buccal cavity depth in females 55, in males 44 ---------- *E.* species A

Palaearctic Species of *Eugenuris* Shul'ts

E. shumakovitschi Shul'ts 1948

E. havliki (Erhardova-Kotrla and Daniel, 1970) new combination

Figure 3. Ventral view of the cloacal region of
a) *Eugenuris* species A, and
b) *E. talkeetnaeuris*. Papillae are
labelled a-h for comparison.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E. pikaeuris (Akhtar, 1953) Akhtar 1956.

3. Notes on Diagnosis

Although the morphological differences are slight, I hesitate to include *E.* species A as a synonym of *E. talkeetnaeuris* because specimens of *E.* species A are usually of smaller size (Tables 5 and 6), and they appear to use different ecological niches within the host (see Chapter VII D).

Seesee (1973) claims that specimens of *E.* species A (which he places in *Dermatoxys*) differ from those of *E. talkeetnaeuris* in having vertical sharp-pointed tooth-like projections on the medial side of the lips, and also in having smaller eggs. The tooth characteristic varies between sexes (Figure 4), but is not diagnostic of the two species. Seesee did not specify the sex of the specimen(s) he used to describe this, and it is not possible to determine the sex from his drawings, because the tooth structures in both sexes are more complex than he has shown. Differences in egg lengths and widths are significant as indicated by Student's t-tests ($p < 0.05$, and $p < 0.001$ respectively; $df = 38$), but means were not as widely divergent as Seesee reported (see Tables 5 and 6, Appendix II).

Grundmann and Lombardi (1976) differentiated specimens of *E. utahensis* from *E. talkeetnaeuris* by tooth structure, and the number and arrangement of cloacal papillae. The tooth characteristic as mentioned above, is not diagnostic

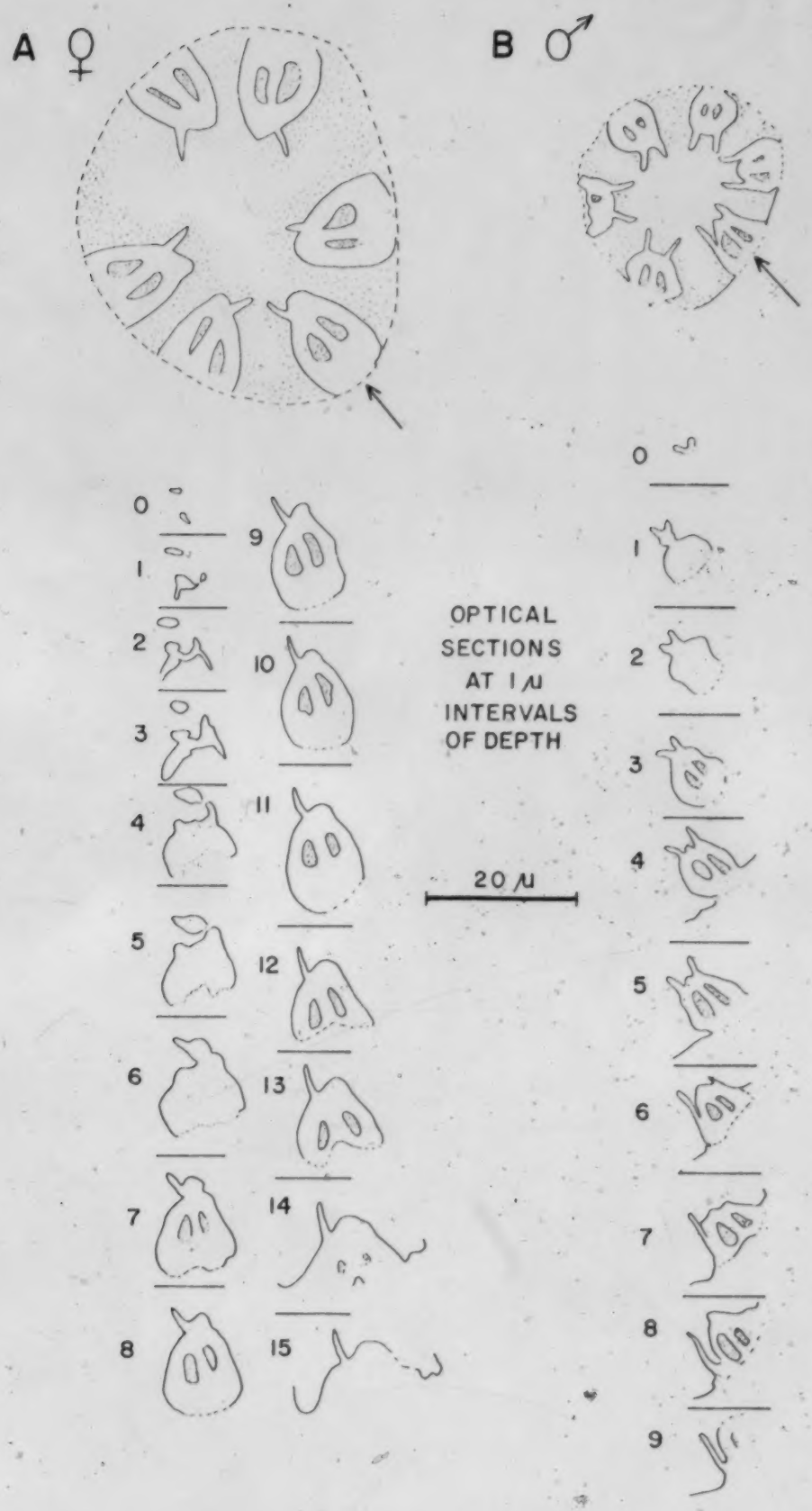
Table 5. Means and 95% confidence limits of measurements of female *Eugenuris* spp. Measurements are in micrometres unless otherwise stated

	Eugenuris sp. A	*E. talkeetnaeuris*	*E. schumakovitschi*
Length (mm)	13.46 ± 1.87	21.25 ± 0.61	20.20 ± 2.48
Width	717 ± 73	955 ± 36	990 ± 170
Striations	10.88 ± 0.88	14.97 ± 0.62	15.09 ± 2.24
Lateral alae width	94.7 ± 14.3	126.8 ± 7.9	130.9 ± 19.0
Oesophagus length	1078 ± 92	1393 ± 26	1431 ± 97
Oesophagus bulb width	190 ± 15	255 ± 10	220 ± 23
Buccal cavity depth	54.7 ± 2.3	62.1 ± 1.7	63.2 ± 7.2
Nerve ring	175 ± 9	199 ± 7	203 ± 10
Head diameter	135 ± 6	143 ± 5	156 ± 5
Tail (mm)	1.74 ± 0.27	2.85 ± 0.07	2.66 ± 0.33
Distance of vulva from anterior end (mm)	6.03 ± 0.81	9.12 ± 0.30	8.97 ± 0.97
Egg length	105.8 ± 1.6	108.4 ± 1.6	111.0 ± 1.8
Egg width	52.5 ± 0.9	55.1 ± 0.7	48.9 ± 0.9

Table 6. Means and 95% confidence limits of measurements of male *Eugenuris* spp. Measurements are in micrometres unless otherwise stated

	Eugenuris sp. A	*E. talkeetnaeuris*	*E. schumakovitschi*
Length (mm)	8.10 ± 0.90	10.46 ± 0.51	11.56 ± 1.23
Width	433 ± 26	451 ± 23	587 ± 84
Striations	8.86 ± 0.58	10.23 ± 0.61	10.93 ± 1.00
Lateral alae width	61.7 ± 3.1	63.7 ± 3.6	71.0 ± 3.5
Oesophagus length	731 ± 49	871 ± 35	994 ± 88
Oesophagus bulb width	141.7 ± 7.5	159.9 ± 8.4	171.7 ± 16.8
Buccal cavity depth	43.9 ± 1.9	51.1 ± 1.6	55.0 ± 2.1
Nerve ring	149.7 ± 7.6	162.8 ± 6.7	169.4 ± 11.9
Head diameter	111.1 ± 6.0	108.6 ± 3.9	121.6 ± 3.0
Tail length (from cloaca)	560 ± 32	677 ± 36	633 ± 47
Tail tip (from caudal alae)	138.6 ± 16.3	153.8 ± 13.5	180.0 ± 25.8
Distance from anterior end of ventral ridge to cloaca	1212 ± 159	1697 ± 108	1846 ± 144

Figure 4. *En face* aspect of a) female, and b) male *Eugenuris talkeetnaeuris*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OPTICAL SECTIONS AT 1 μ INTERVALS OF DEPTH
20 μ

of the species. The arrangement of the cloacal papillae shown in figure 5 of Grundmann and Lombardi (1976) is similar to that for specimens of *E.* species A, except that the "e" and "f" papillae are misinterpreted as the cloacal opening, and a small papilla is shown where the cloaca should be.

The distinguishing characteristics I have used in the key (eggs and uterus), are open to question, as these structures are otherwise known as stable characters for all the pinworms of pikas. Regarding the egg character, Yamaguti (1961: 545) (apparently due to an error in translation) stated that eggs of *E. schumakovitschi* Shul'ts 1948 are operculated at each pole instead of at one pole. Eggs of all other pika pinworms are operculated at one pole, and are distinguishable only by size. Similarly, the structure of the uterus in pika pinworms with the sole exception of *E. utahensis* is as described in the key above for members of *E.* species A. The uterus loop in figure 4 of Grundmann and Lombardi (1976) may be a misinterpretation of the glandular structure which encircles the ovejector in other pika pinworms.

Akhtar (1956b) constructed a key to distinguish among the three species of *Eugenuris* known at that time. However the characteristics he used were not diagnostic: specimens of both *E. schumakovitschi* and *E. talkeetnaeuris* have indented lips in the sense of Shul'ts (1948), and the supposed differences in lip and tooth structure between specimens of the

latter species and those of *E. pikaeuris* are illusory.

Erhardova-Kotrla and Daniel (1970) attempted to differentiate among the species on the basis of the oral structures, but their statements are in part incorrect and in part contradictory. They also indicate that members of *E. havliki* possess only three lips, and if so, this species probably belongs in another genus. However, the oral structures were probably mis-interpreted because otherwise the characteristics of *E. havliki* fit those of *Eugenuris*.

In conclusion, the Nearctic species *E. talkeetnaeuris* seems to be clearly distinguished from *E. utahensis* and *E.* species A, but members of the latter two species may be conspecific. The Palaearctic species are not well understood. Specimens of *E. schumakovitschi* (two series - one collected from *O. rutila* in Kazakhstan by E.V. Gvozdev; the other from *O. hyperborea yesoensis*, collected by F.C. Zwickel) are very similar to both American species in oral structures. Sizes of the Kazakhstan series are more similar to those of *E. talkeetnaeuris* specimens than *E.* species A (Table 5). More work needs to be done to determine the significance of these similarities.

Since I have not seen specimens of either *E. havliki* or *E. pikaeuris*, and details of the oral structures and cloacal papillae are lacking from the descriptions, I cannot determine their relationships to one another or to the other species. Clearly additional work is required to elucidate the Palaearctic species.

4. Host Records and Geographical Distribution

In the Nearctic, members of *E. talkeetnaeuris* are known from specimens of *O. collaris* in Alaska (Akhtar, 1956b - type area), and the Yukon Territory (this study). Specimens of *Eugenuris* species A are known from *O. princeps* specimens in Alberta (this study) and Idaho (Seesee, 1973). Members of *E. utahensis* are known from *O. princeps* specimens in Utah and Nevada (Grundmann and Lombardi, 1976). *Eugenuris* species are known from *O. princeps* specimens from Oregon (Roest, 1953) and California (Voge, 1956).

Distributional data for the Palaearctic species are presented in Table 7.

Labiostomum Akhtar 1941

Labiostomum Akhtar 1941: 217. TYPE SPECIES:- *L. naimi* Akhtar 1941 (by monotypy).

Five species are included in this genus, two in the Nearctic, and three in the Palaearctic. The following key distinguishes among them.

Key to the Species of *Labiostomum* Akhtar

1A. Papilla immediately posterior to cloaca in males ("e"), quadruple ---------- ---------- *L. akhtari* Inglis 1959

1B. "e" papilla not quadruple, usually double ---------- (2)

2A. Cephalic bulb diameter greater than 250 micrometres in females, and greater than 200 in males; Palaearctic distribution ---------- (3)

Table 7. Host records and data on geographic distribution of the Palaearctic species of *Eugenuris* Shul'ts

Host	*E. schumakovitschi*	*E. pikaeuris*	*E. havliki*
Ochotona rufescens	x[1]	x[8]	
O. roylei			x[9]
O. rutila	x[2]		
O. alpina	x[3]	—	
O. hyperborea	x[4]		
O. daurica	x[5]		
O. macrotis	x[6]		
O. pallasi	x[7]		

1-9 Localities: 1. Turkmenia (Babaev, 1967); 2. Kirghizii (Tokobaev, 1960), Kazakhstan (this study); 3. Zabaikal (Dubinin and Dubinina, 1951), Pribaikal (Spasskii and Ryzhikov, 1951), Altai Mountains (Gvozdev, 1951), and central Kazakhstan (Gvozdev, 1956); 4. Yakutia (Gubanov, 1964); 5. Mongolia (Shul'ts, 1948 - type area; Meszaros, 1974), Zabaikal (Dubinin and Dubinina, 1951); 6. Tyan Shan (Gvozdev, 1964), Kirghizii (Tokobaev, 1960); 7. central Kazakhstan (Gvozdev, 1956); 8. Afghanistan (Akhtar, 1953 - type area; Barus et al., 1972); 9. Hindu Kush (Erhardova-Kotrla and Daniel, 1970 - type area).

2B. Cephalic bulb diameter less than 250 micrometres in females, and less than 200 in males; Nearctic distribution ---------- (4)

3A. 11 pairs of cloacal papillae in males ---------- *L. naimi* Akhtar 1941

3B. 6 pairs of cloacal papillae --------- ---------- *L. vesicularis* Gvozdev 1956

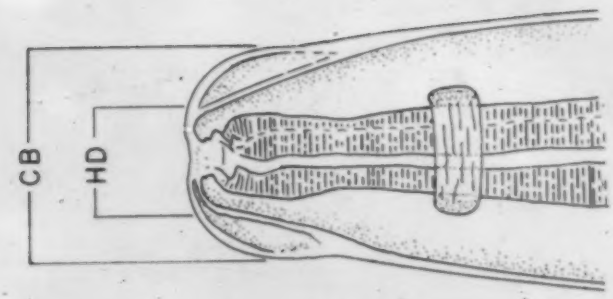
4A. Inner head diameter less than 93 micrometres in females and less than 75 in males (Figure 5a); distance from cloacal vent to tip of tail in males less than 550 micrometres ----- ---------- *L. coloradensis* Leiby 1961

4B. Inner head diameter greater than 93 micrometres in females, and greater than 75 in males; distance from cloacal vent to tail tip in males greater than 550 micrometres -------- ---------- *L. rauschi* Akhtar 1956

1. Notes on Diagnosis

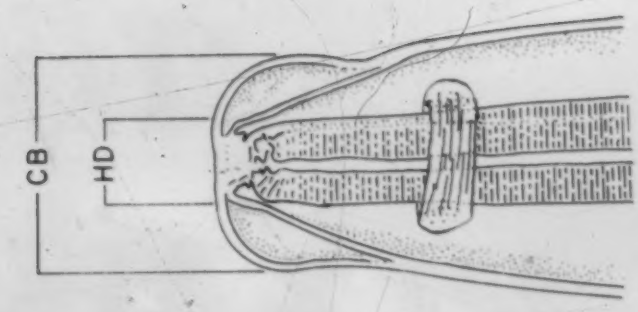
Members of the Nearctic species were differentiated by Leiby (1961b) according to size. Males of *L. coloradensis* were smaller than males of *L. rauschi*. However, males of *L. coloradensis* I have seen from the same host species, close to the type locality, were about three times the length of those in the type series (Table 9, and Appendix III); the latter specimens were apparently immature. Another character Leiby used was "different arrangement of the ventral crests". I am not sure what this means, but the ridge extends closer to the cloacal vent in specimens of *L. coloradensis* than in *L. rauschi* specimens (analysis of covariance: $p < 0.005$ for both regression on body length, and difference of means).

Figure 5. Lateral aspect of anterior end of a) *Labiostomum coloradensis*, and b) *L. rauschi*. (CB - cephalic bulb diameter, HD - head diameter).



B

200 μ



A

Seesee (1973) gave a brief and incomplete description of specimens belonging to *Labiostomum*, from *O. princeps* in Idaho, which he claimed differed from members of *L. coloradensis* by the greater body length in males, the tooth structure, and the presence of a spicule in males. As mentioned above, I consider that the males Leiby measured were immature, so Seesee's first characteristic is invalid. Seesee did not give the size of his specimens, except that they were longer than 10 mm. Specimens of *L. coloradensis* that I measured averaged 10.6 mm. Regarding the second character, Seesee claimed that Leiby had described specimens of *L. coloradensis* with a tooth-like projection at the very tip of each lip. Leiby clearly did not describe the teeth that way: "in *L. coloradensis* they [the tooth-like projections] extend anterolaterally from the adjacent sides of the paired lips." Seesee is not explicit about the tooth structure in his specimens, but his figure (figure 5 of Seesee, 1973) may easily be interpreted to illustrate what Leiby described. Finally, it is extremely unlikely that Seesee saw a spicule in his specimens. No other members of either *Labiostomum*, *Eugenuris* or *Cephaluris*, all closely related worms, have a spicule, although some were originally described as having one. The cuticular lining of the rectum in some cases looks like a spicule, and it is clear that Seesee has misinterpreted this structure. Therefore, this species is *L. coloradensis*.

Males of the Palaearctic species *L. naimi* are supposed

to have more cloacal papillae (11 pairs according to Akhtar, 1941) than males of *L. coloradensis*, but this may not be so because only six pairs are shown in Akhtar's (1941) ventral view (Akhtar's figure 2a). Males of *L. naimi* are also much shorter than the males of *L. coloradensis* which I measured (Table 9, and Appendix III), but Akhtar appears to have described immature specimens as indicated by the meagre development of the caudal alae (figures 2a and 2b of Akhtar). According to Leiby (1961b) males of *L. coloradensis* have a shorter ventral crest than males of *L. vesicularis*. This character, however, is highly variable.

Leiby (1961b) differentiated *L. coloradensis* from *L. akhtari* by position of the tooth-like projections on the lips: among specimens of the former species, these structures project from the side of the lip, whereas in specimens of the latter species they project from the midline. There is a marked sex difference in this character in specimens of *L. coloradensis*, not noted by Leiby, but it does apply to both sexes. Additionally, males of *L. coloradensis* have a double, not a quadruple papilla immediately posterior to the cloacal vent.

Akhtar (1956b) used six characters to distinguish between specimens of *L. rauschi* and *L. naimi*. Three of these are valid: specimens of *L. rauschi* have a smaller cephalic bulb, larger eggs, and longer body size (Tables 8 and 9; Appendix III). Another character (fewer cloacal papillae in males of *L. rauschi*) may also be valid, but

Table 8. Means and 95% confidence limits of measurements of female *Labiostomum* spp. Measurements are in micrometres unless otherwise stated

	L. coloradensis	*L. rauschi*	*L. vesicularis*
Length (mm)	17.92 ± 0.68	18.36 ± 0.63	20.45 ± 2.32
Width	759 ± 30	803 ± 27	753 ± 78
Striations	21.0 ± 1.0	21.3 ± 1.1	23.3 ± 3.5
Lateral alae width	105.4 ± 4.2	133.0 ± 7.2	142.8 ± 15.3
Oesophagus length	1431 ± 35	1429 ± 34	1538 ± 172
Oesophagus bulb width	203 ± 7	209 ± 6	207 ± 33
Buccal cavity depth	59.1 ± 1.8	61.6 ± 1.3	59.5 ± 4.8
Nerve ring	203 ± 5	210 ± 4	213 ± 26
Head diameter	88.7 ± 2.3	97.2 ± 2.3	88.3 ± 12.3
Cephalic bulb diameter	216 ± 6	222 ± 4	287 ± 24
Tail (mm)	2.11 ± 0.09	2.09 ± 0.08	2.14 ± 0.15
Distance of vulva from anterior end (mm)	8.17 ± 0.38	8.49 ± 0.36	9.65 ± 1.31
Egg length	93.1 ± 1.3	97.1 ± 1.3	100.5 ± 2.7
Egg width	49.3 ± 0.6	52.3 ± 0.8	48.1 ± 1.3

Table 9. Means and 95% confidence limits of measurements of male *Labiostomum* spp. Measurements are in micrometres unless otherwise stated

	L. coloradensis	*L. rauschi*	*L. vesicularis**
Length (mm)	10.64 ± 0.37	10.71 ± 0.52	12.2
Width	421 ± 12	423 ± 21	0.52
Striations	14.4 ± 0.8	14.9 ± 1.3	15.0
Lateral alae width	57.3 ± 3.4	67.7 ± 3.0	73.0
Oesophagus length	953 ± 24	964 ± 35	1035
Oesophagus bulb width	141.0 ± 4.5	145.3 ± 6.0	154.5
Buccal cavity depth	47.2 ± 1.2	48.1 ± 1.1	47.0
Nerve ring	168.4 ± 3.6	172.5 ± 3.8	178.0
Head diameter	72.9 ± 1.6	79.5 ± 2.4	77.5
Cephalic bulb diameter	170.9 ± 5.2	170.3 ± 4.9	210.0
Tail length (from cloaca)	526 ± 16	594 ± 27	480
Distance from anterior end of ventral ridge to cloaca	1138 ± 88	1025 ± 54	1125

* Sample size (n = 2) is too small for meaningful confidence limits.

Akhtar (1941) was inconsistent with his diagrams of specimens of *L. naimi*, as mentioned above. Two characters are not useful: length of oesophagus (correlated with body size), and length of tail in females.

Members of *L. rauschi* differ from those of *L. vesicularis* and *L. akhtari* by characters shown in the key.

Among the Palaearctic species, *L. naimi* males differ from males of the other species by possession of 11 pairs of cloacal papillae. As mentioned above, this may be incorrect. Other characters reported as diagnostic between specimens of *L. naimi* and *L. vesicularis* (absence of a spicule, structure of the buccal cavity, body length in males (Gvozdev, 1956)) are not useful. Males of *L. akhtari* are distinguished by possession of a quadruple medial papilla, just posterior to the cloacal vent (Inglis, 1959).

2. Host Records and Geographical Distribution

Members of the Nearctic *L. coloradensis* are known from *O. princeps* in Colorado (Leiby, 1961b - type area), Utah (Warnock, 1962; Grundmann and Lombardi, 1976), Nevada (Grundmann and Lombardi, 1976), Montana (Barrett and Worley, 1970), Idaho (Seesee, 1973), and Alberta (this study). Members of *L. rauschi* are known from *O. collaris* from Alaska (Akhtar, 1956b - type area), and Yukon Territory (this study).

Distributional data for the Palaearctic species are presented in Table 10.

Table 10. Host records and data on geographic distribution of the Palaearctic species of *Labiostomum* Akhtar

Host	*L. naimi*	*L. vesicularis*	*L. akhtari*
Ochotona rufescens	x[1]	x[3]	x[10]
O. hyperborea	(x[2]?)	x[4]	
O. macrotis		x[5]	
O. pallasi		x[6]	
O. daurica		x[7]	
O. rutila		x[8]	
O. alpina		(x[9]?)	

1-10 Localities: 1. Afghanistan (Akhtar, 1941 - type area), Turkmenia (Babaev, 1967); 2. lower Lena region (Kapitonov, 1961); 3. Turkmenia (Babaev, 1967); 4. Taymyr (Mustafaev, 1968); 5. Tyan Shan (Gvozdev, 1964); 6. central Kazakhstan (Gvozdev, 1956 - type area); 7. eastern Mongolia (Meszaros, 1974); 8. Kazakhstan (this study); 9. Pribaikal (Spasskii and Ryzhikov, 1951: reported as "*Eugenuris* sp.", but is probably *L. vesicularis*; 10. Iran (Inglis, 1959 - type area), Turkmenia (Babaev, 1967).

CHAPTER VI

ECOLOGY: GROUPS OF HOSTS

In this chapter, I consider the dynamics of populations and communities of helminths in groups of hosts, in order to ascertain the effects of extrinsic modifying factors.

A. Analytical Methods

Various measures are used to compare helminth populations and communities of different groups of hosts. These are:

1. The abundance index (Z) (Janion, 1968). It is calculated as:

$$Z_i = \frac{a \times b}{c^2}$$

where a = the total number of individuals of helminth species i,

b = the number of hosts infected with species i,

c = the number of hosts examined.

This index is used in graphical representations of helminth abundances, because it incorporates both prevalence and intensity. Since only one value of Z exists for a group of hosts, it is not amenable

to statistical analysis.

2. A logarithmic transformation of intensity of infection:

$$\log_{10} (N_i + 1)$$

where N_i is the number of individuals of species i in an individual host. It is used in the statistical comparisons of abundance. Uninfected hosts are included in the analyses unless otherwise indicated.

3. The importance value (D_i) (Bush, 1973). It is calculated as:

$$D_i = \frac{Z_i \times 100}{\sum_{i=1}^{S} Z_i},$$

where D_i is the percent importance of species i, and Z_i is the abundance index for species i, in a community of S species.

4. Species richness (S), the number of species in the community.

5. The Shannon-Weaver (1949) index of diversity (H'). It is calculated as:

$$H' = - \sum_{i=1}^{S} p_i \ln p_i ,$$

where p_i is the proportion of the community of S species represented by species i, and ln is the logarithm of base e. H' is influenced by changes in both components of diversity, species richness and relative abundance (equitability).

6. Equitability (J) (Pielou, 1969). It is calculated as:

$$J = \frac{H'}{H'_{max}}$$

where H' is the Shannon-Weaver diversity index, and $H'_{max} = \ln S$.

I use "infrapopulation" in the same sense as Esch et al. (1975), to include "all individuals of a single parasite species within an individual host." Esch et al. (1975) used "suprapopulation" to include "all parasites of a given species, in all stages of development, within all hosts of an ecosystem." Since the boundaries of an ecosystem are usually nebulous, a suprapopulation in the above sense is difficult to define. Thus, I have taken the liberty of redefining the term for the purposes of this study, to include the members of a given species of helminth within a given group of hosts. Additionally, I have extended these categories to the community level, such that individuals of all helminth species within an individual host comprise an infracommunity, and individuals of all helminth species within a given group of

hosts comprise a supracommunity.

Statistical analyses were performed on groups of infracommunity diversities, and infrapopulation abundances. Either one-way (Steel and Torrie, 1960: p. 112) or two-way (Steel and Torrie, 1960: p. 269) analyses of variance (ANOVA) were carried out. In the former case, if a significant ($p \leq 0.05$) F value for treatments was obtained, means were differentiated by a Duncan's Multiple Range Test (Steel and Torrie, 1960: p. 107). The method used to differentiate means in a two-way ANOVA was that in Steel and Torrie (1960: p. 271).

Intensity frequency distributions of helminths were compared with Poisson frequency tables (Beyer, 1968), and negative binomial distributions, the component k of which was fitted by an iterative method of Bliss and Fisher (1953). Statistical comparison of these distributions was by Chi-square tests (Steel and Torrie, 1960: p. 349).

The two species of *Cephaluris* were pooled for the analyses, because females were indistinguishable from each other (p. 30).

B. General Description

Considering the helminths of all sampled individuals of a host species to represent a supracommunity, the two such communities are remarkably similar in diversity (Table 11). The *Ochotona princeps* (= Alberta) supracommunity has greater species richness and this raises the diversity, but equit-

Table 11. Comparison of diversity values for both supracommunities, considering worms from all hosts of each species as the community

Diversity measure	Community		t-value for difference of means
	Ochotona princeps	*O. collaris*	
Supracommunity			
H'	1.44	1.09	
S	6	4	
J	0.804	0.787	
Infracommunity mean			
H'	0.704	0.656	0.842
S	3.18	2.63	2.63**
J	0.564	0.588	0.539

** $p < 0.01$

ability is almost identical to that of the supracommunity in *O. collaris* (= Yukon). When means of diversity values for infracommunities are considered for the two host species, only species richness is significantly different between groups. See Section D for a more complete discussion.

In contrast to the above findings, species composition of the two supracommunities is quite different (Table 12). The *O. princeps* supracommunity is dominated by *Murielus harpespiculus*, which is not present in the *O. collaris* supracommunity; *Cephalurus* spp. dominate the latter supracommunity.

Bush (1973) proposed a scheme of dominance, based on his importance index, in which helminths are categorized in a decreasing scale as dominants, co-dominants, successful immigrants and unsuccessful immigrants. Species with D_i values greater than or equal to 1.0, he called dominants; those with $0.01 < D_i < 1.0$, co-dominants. He suggested that while dominants are characteristic of the community, co-dominants may do well in other habitats. According to this hypothesis, all helminth species in pikas should be dominants, because none are known to survive in other habitats (= other sympatric host species), even as unsuccessful immigrants. My data support his hypothesis: even the least abundant species *Labiostomum rauschi* and *L. coloradensis* are classified as dominants (Table 12).

The abundance index and values of mean intensity reveal nothing of the way in which the helminths are distributed amongst host individuals. Many workers have found

Table 12. Species composition of the two supracommunities

Community	Helminth Species	Prevalence (%)	Z	D	Mean Intensity*	Range (Intensity)
Ochotona princeps	*Schizorchis caballeroi*	67.6	2.43	9.7	5.3	1-28
	Graphidiella ochotonae	47.8	1.12	4.5	4.9	1-30
	Murielus harpespiculus	48.7	9.70	38.8	41.0	1-186
	Eugenuris sp. A	50.5	3.36	13.4	13.2	1-134
	Labiostomum coloradensis	25.2	0.29	1.1	4.5	1-14
	Cephaluris spp.	78.4	8.11	32.4	13.2	1-75
Ochotona collaris	*Schizorchis caballeroi*	77.2	8.31	27.0	14.0	1-103
	Eugenuris talkeetnaeuris	70.7	4.55	14.8	9.1	1-68
	Labiostomum rauschi	32.6	0.39	1.3	3.7	1-15
	Cephaluris spp.	82.6	17.50	56.9	25.6	1-123

* Number of helminths/number of hosts infected.

that helminths are usually clumped, such that a small proportion of hosts carry the greater part of the helminth population (Li and Hsu, 1951; Northam and Rocha, 1958; Froyd and Clark, 1962; Bradley, 1965; Thomas, 1965; Kisielewska, 1970b; Crofton, 1971a, 1971b; Pennycuik, 1971; Bush, 1973; Anderson, 1974). Intensity frequency distributions of all helminth species, except *Labiostomum rauschi* in *O. collaris*, show a good fit to the negative binomial distribution, and all show a poor fit to the Poisson (Table 13, see Figure 6 for an example). Thus, individual helminths are over-dispersed, or clumped.

Factors responsible for clumping may be:

(i) seasonality in abundance,

(ii) resistance or specificity, related to host age,

(iii) resistance or specificity, related to host sex,

(iv) locational differences in abundance,

(v) clumping of infective stages,

(vi) interspecific interactions.

Each of the first five of these causes will be discussed in the remainder of this chapter, and the sixth cause in the Chapter VII.

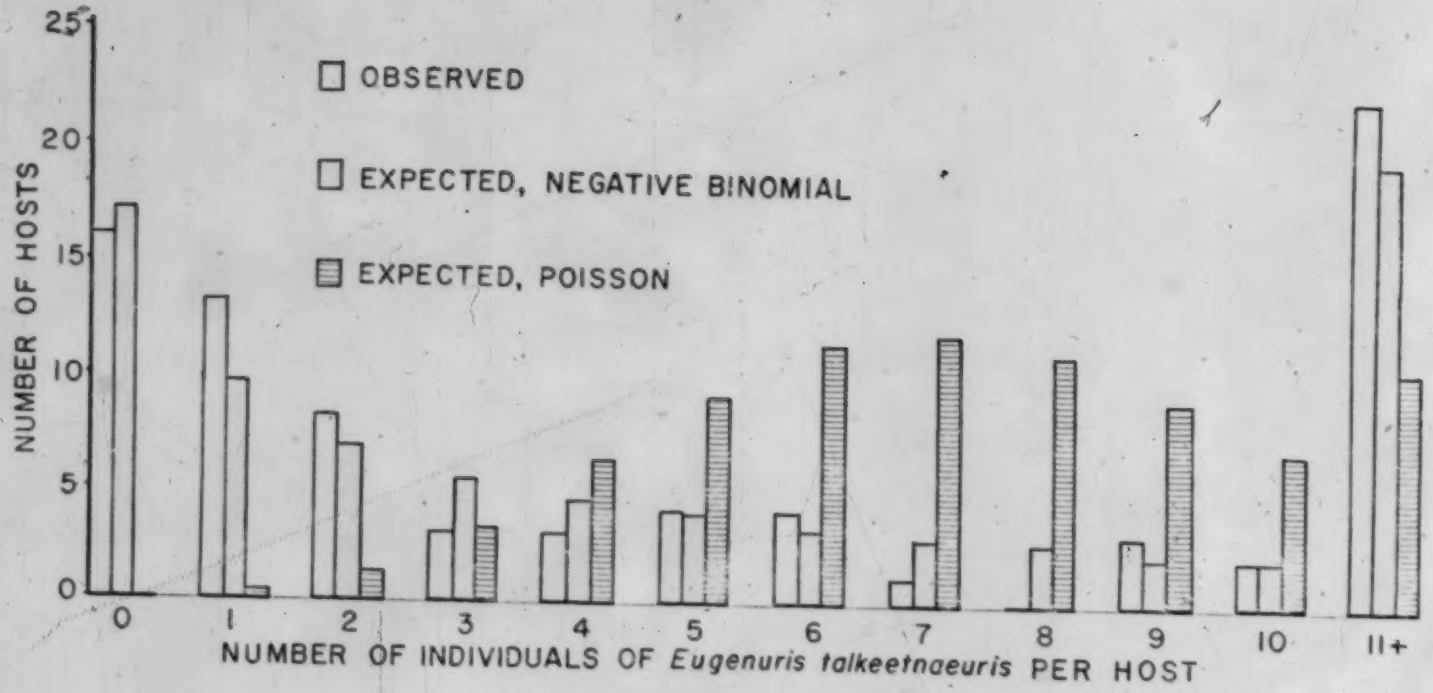
C. Season and Sex

No significant changes in diversity due to season adjusted for sex were found for either the *O. princeps* or *O. collaris* supracommunities. However, there were sex differences for both supracommunities, in species richness,

Table 13. Chi-squared probabilities of helminth intensity frequency distributions being different from Poisson, and negative binomial distributions. The k components for expected negative binomial distributions are also listed. Only adult pikas were included in the analyses.

Host	Helminth	Poisson	Negative Binomial	k
Ochotona princeps	*Schizorchis caballeroi*	$p < 0.005$	$p > 0.5$	0.907
	Graphidiella ochotonae	$p < 0.005$	$p > 0.5$	0.411
	Murielus harpespiculus	$p < 0.005$	$p > 0.1$	0.390
	Eugenuris sp. A	$p < 0.005$	$p > 0.1$	0.253
	Labiostomum coloradensis	$p < 0.005$	$p > 0.5$	0.175
	Cephaluris spp.	$p < 0.005$	$p > 0.5$	0.837
Ochotona collaris	*Schizorchis caballeroi*	$p < 0.005$	$p > 0.1$	0.586
	Eugenuris talkeetnaeuris	$p < 0.005$	$p > 0.1$	0.575
	Labiostomum rauschi	$p < 0.005$	$p < 0.05$	0.258
	Cephaluris spp.	$p < 0.005$	$p > 0.1$	0.979

Figure 6. Intensity frequency distribution of *Eugenuria talkeetnaeuria* in adult *Ochotona collaris*, compared with expected Poisson and negative binomial distributions.


OBSERVED
EXPECTED, NEGATIVE BINOMIAL
EXPECTED, POISSON
NUMBER OF HOSTS
25
20
15
10
5
0
0
1
2
3
4
5
6
7
8
9
10
11+
NUMBER OF INDIVIDUALS OF Eugenuris talkeetnaeuris PER HOST

and Shannon-Weaver diversity (Figure 7). Females of *O. princeps* have consistently more diverse helminth communities than males; species richness was also higher except for one sample. The pattern for *O. collaris* helminth communities is much more complex. Trends seen in species richness are reflected in the diversity index. Values for helminths in female hosts fluctuate more than for those in males, but this may be due to the lower sample sizes of females.

Each helminth species is now considered separately (Figure 8). Only one species group (a pair of species) referred to as *Cephaluris* spp. in *O. princeps* showed any significant seasonal trend, and only one sample, the first, caused this difference (Figure 8d). Although *Cephaluris* spp. was the only one to show a statistically significant seasonal trend all nematode species in *O. princeps* were low in abundance at the first collection period. Thus, there is probably a reduced exposure to infective stages late in the winter. Data from seven pikas collected in mid-November, not included in the analysis, show that mean intensities of pinworms are quite high at that time (Table 14). Furthermore, the pika captured on 21st December was heavily infected, whereas the pika collected on 3rd April had few pinworms (Table 14). It is not worthwhile at the present time to speculate on the rate of acquisition of new infections during winter, as longevities of worms are unknown for all species.

Table 14. Mean intensities of helminths in winter-collected *Ochotona princeps*

Helminth	November 13-15 (n = 7)		December 21 (n = 1)	April 3 (n = 1)
Schizorchis caballeroi	3.8*	(4)**	1	2
Graphidiella ochotonae	6.0	(7)	1	13
Murielus harpespiculus	9	(1)	0	134
Eugenuris sp. A	5.7	(3)	27	7
Labiostomum coloradensis	1	(1)	14	0
Cephaluris spp.	16.9	(7)	31	6

* Total number of worms/number of pikas infected.

** Number of pikas infected.

Figure 7. Mean Shannon-Weaver diversity values (H'), mean number of species, and analysis of variance for infracommunities of helminths in adult pikas, at different collection periods. Median collection dates for each period and sample sizes (male hosts, female hosts) are as follows

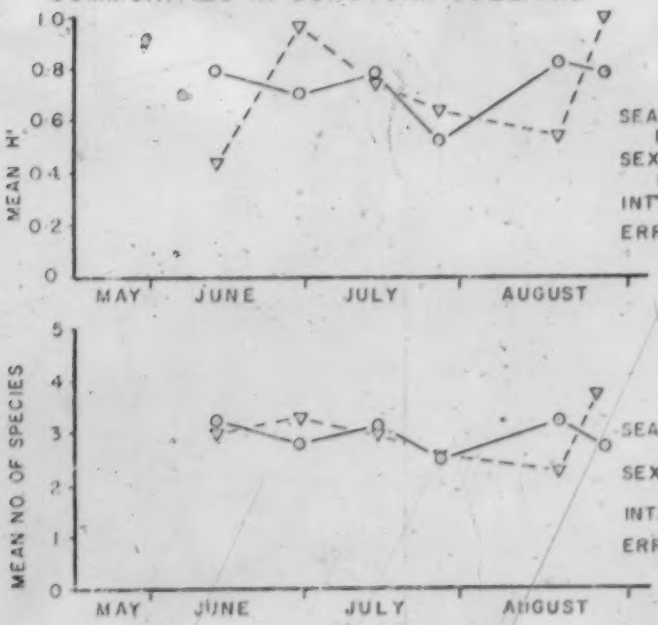
Ochotona collaris:
14 June (11, 3)
30 June (11, 3)
15 July (7, 4)
27 July (2, 11)
12 August (8, 7)
28 August (8, 4)

Ochotona princeps:
1 June (12, 6)
28 June (18, 5)
22 July (11, 6)
14 August (10, 11)

○———○ Male hosts

▽— — —▽ Female hosts

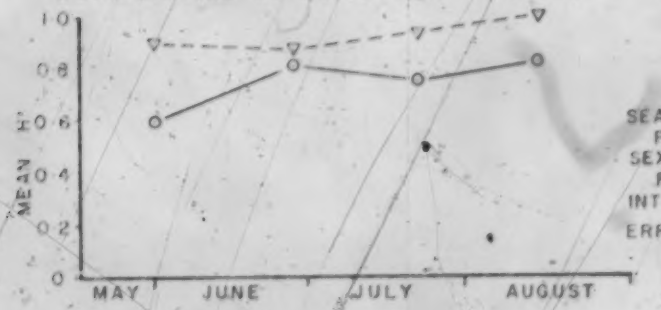
COMMUNITIES IN *OCHOTONA COLLARIS*



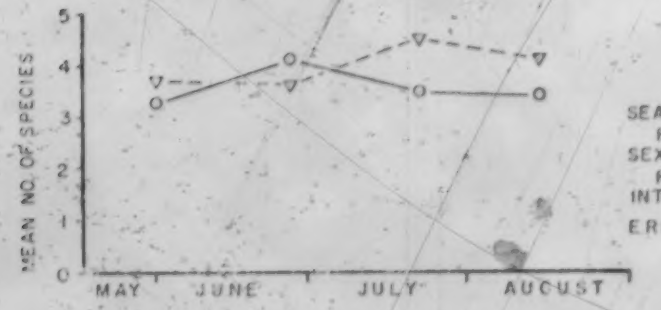
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0·157	1·34	N.S.
SEX, ADJUSTED FOR SEASON	1	0·801	6·84	$P<0.025$
INTERACTION	5	0·033	0·28	N.S.
ERROR	67	0·117		

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0·646	0·74	N.S.
SEX, ADJUSTED FOR SEASON	1	4·740	5·43	$P<0.025$
INTERACTION	5	0·441	0·51	N.S.
ERROR	67	0·872		

COMMUNITIES IN *OCHOTONA PRINCEPS*



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	3	0·113	1·05	N.S.
SEX, ADJUSTED FOR SEASON	1	0·634	5·90	$P<0.025$
INTERACTION	3	0·038	0·35	N.S.
ERROR	71	0·107		



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	3	0·756	0·60	N.S.
SEX, ADJUSTED FOR SEASON	1	7·275	5·82	$P<0.025$
INTERACTION	3	0·317	0·25	N.S.
ERROR	71	1·250		

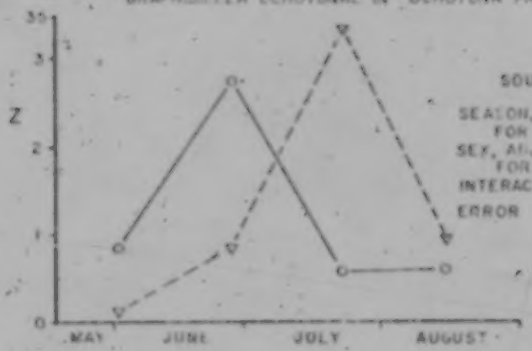
Figure 8. Abundance values (Z) for suprapopulations, and analysis of variance on $\log_{10}$ (N + 1) for infrapopulations of helminths in adult pikas at different collection periods. Median collection dates and sample sizes are as in Figure 7. a) *Graphidiella* and *Murielus*, b) *Labiostomum*, c) *Eugenuris*, d) *Cephaluris*, and e) *Schizorchis*.

⊙———⊙ Male hosts

▽— — —▽ Female hosts

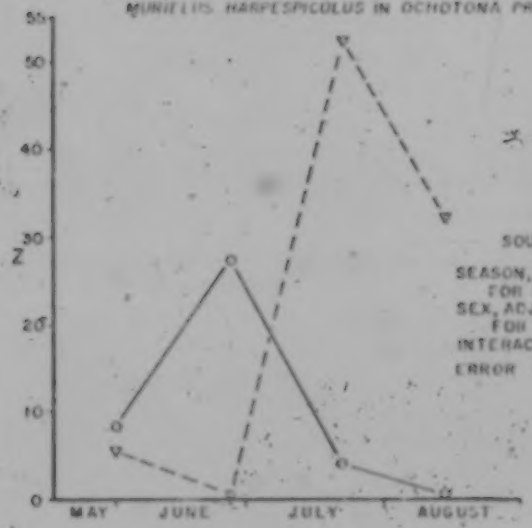
8 A

GRAPHIURILLA OCHOTONAE IN OCHOTONA PRINCEPS



SOURCE	DF	MEAN SQUARE	F	SIGN
SEASON, ADJUSTED FOR SEX	3	0.069	0.45	N.S.
SEX, ADJUSTED FOR SEASON	1	0.768	5.07	P<0.05
INTERACTION	3	0.125	0.83	N.S.
ERROR	71	0.152		

MUNIELLUS HARPESPICULUS IN OCHOTONA PRINCEPS



SOURCE	DF	MEAN SQUARE	F	SIGNIF
SEASON, ADJUSTED FOR SEX	3	0.243	0.42	N.S.
SEX, ADJUSTED FOR SEASON	1	7.242	12.58	P<0.005
INTERACTION	3	0.733	1.27	N.S.
ERROR	71	0.566		

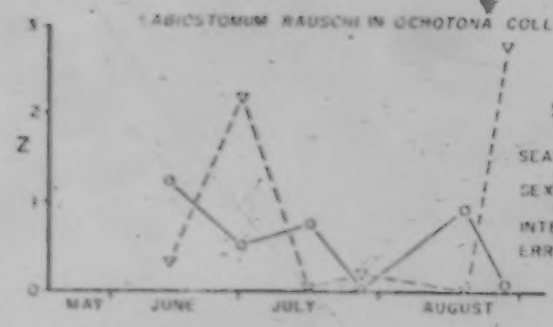
Figure 8. Continued

⊙———⊙ Male hosts

▽— — —▽ Female hosts

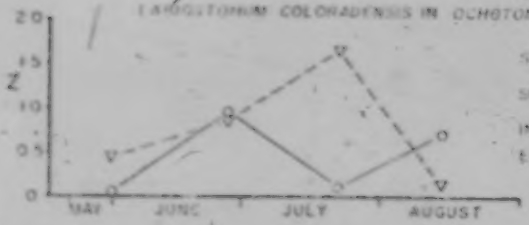
8B

LABIDOSTOMUM RAUSCHI IN OCHOTONA COLLARIS



SOURCE	DF	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.138	1.43	N.S.
SEX, ADJUSTED FOR SEASON	1	1.023	10.63	P<0.005
INTERACTION	5	0.044	0.46	N.S.
ERROR	67	0.096		

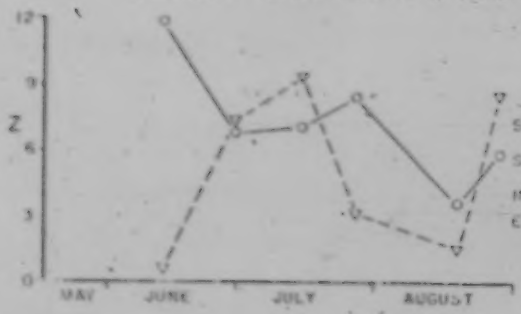
LABIDOSTOMUM COLORADENSIS IN OCHOTONA PRINCEPS



SOURCE	DF	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.185	0.23	N.S.
SEX, ADJUSTED FOR SEASON	1	0.438	3.87	N.S.
INTERACTION	5	0.054	0.47	N.S.
ERROR	71	0.85		

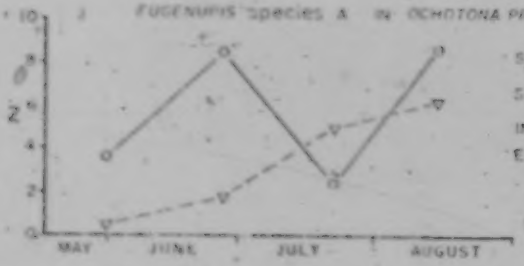
8C

EUGENURUS TALKEETNAENSIS IN OCHOTONA COLLARIS



SOURCE	DF	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.322	1.36	N.S.
SEX, ADJUSTED FOR SEASON	1	1.064	4.51	P<0.05
INTERACTION	5	0.081	0.34	N.S.
ERROR	67	0.236		

EUGENURUS species A IN OCHOTONA PRINCEPS



SOURCE	DF	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.319	0.99	N.S.
SEX, ADJUSTED FOR SEASON	1	0.852	2.66	N.S.
INTERACTION	5	0.018	0.05	N.S.
ERROR	71	0.320		

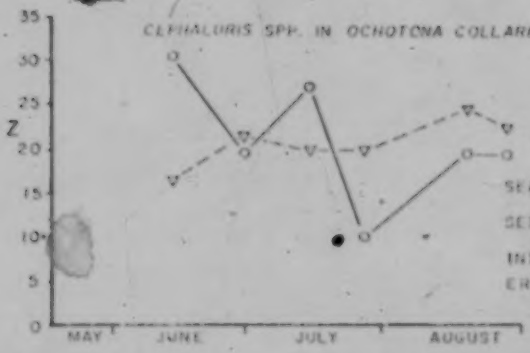
Figure 8. Continued

⊙———⊙ Male hosts

▽— — —▽ Female hosts

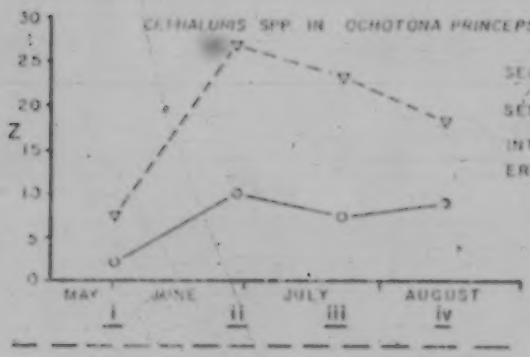
8 D

CEPHALURIS SPP. IN OCHOTONA COLLARIS



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.062	0.20	N.S.
SEX, ADJUSTED FOR SEASON	1	0.429	1.41	N.S.
INTERACTION	5	0.023	0.07	N.S.
ERROR	67	0.304		

CEPHALURIS SPP. IN OCHOTONA PRINCEPS

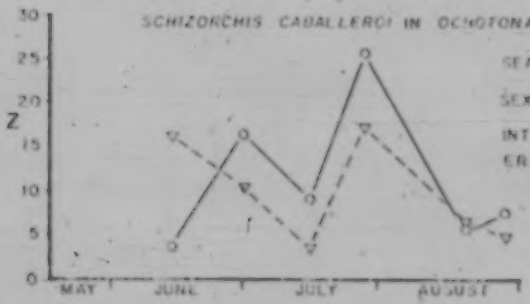


SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	3	0.660	3.40	$P<0.05$
SEX, ADJUSTED FOR SEASON	1	2.548	13.11	$P<0.005$
INTERACTION	3	0.015	0.08	N.S.
ERROR	71	0.194		

i iv iii ii

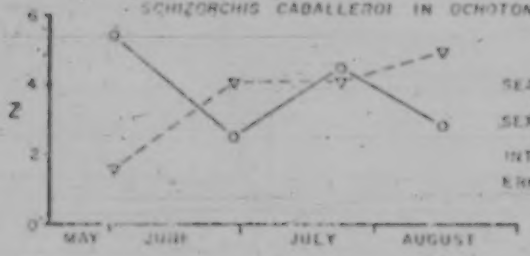
8 E

SCHIZORCHIS CABALLEROI IN OCHOTONA COLLARIS



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	5	0.084	0.29	N.S.
SEX, ADJUSTED FOR SEASON	1	0.299	1.02	N.S.
INTERACTION	5	0.033	0.11	N.S.
ERROR	67	0.293		

SCHIZORCHIS CABALLEROI IN OCHOTONA PRINCEPS



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
SEASON, ADJUSTED FOR SEX	3	0.051	0.32	N.S.
SEX, ADJUSTED FOR SEASON	1	0.595	3.79	N.S.
INTERACTION	3	0.029	0.18	N.S.
ERROR	71	0.157		

Two species in *O. collaris* helminth communities (*Eugenuris talkeetnaeuris* and *Labiostomum rauschi*) and three in *O. princeps* communities (*Graphidiella ochotonae*, *Murielus harpespiculus* and *Cephaluris* spp.) were significantly different (two-way analysis of variance) in abundance between host-sex grouping, when adjusted for season (Figure 8).

In *O. princeps*, the two trichostrongyloids (*G. ochotonae* and *M. harpespiculus*) show similar patterns, such that populations reach a peak earlier in males than in females (Figure 8a). Female pikas did not maintain high populations of helminths until after the breeding season. This is opposite to the case with two trichostrongyloids, *Trichostrongylus retortaeformis* and *Graphidium strigosum*, in rabbits (*Oryctolagus cuniculus*) in Australia investigated by Dunsmore (1966a, 1966b) and Dunsmore and Dudzynski (1968), and with *T. retortaeformis* in wild rabbits in New Zealand (Bull, 1964). Dunsmore (1966d, 1971) showed experimentally that the increase in worm burdens in females during the breeding season were due to host hormones, including ACTH and probably oestrogen. He postulated that either the immunological threshold varies with different hormonal states, or hormones change the microhabitat of the gut. Transmission to young hosts is made maximum because the highest levels, and hence the highest production of infective stages, are attained in females at the period of greatest contact with young.

One would expect this to be true for pikas too. That it is not so could result from females being under more stress after the breeding period than during it. At the end of the breeding period, they must compete with males for territory and begin collecting hay. Males on the other hand, get an earlier start with hay collecting (Sharp, 1973). Perhaps the greatest stress for males is during the breeding season when they defend larger territories, which they share with females (Sharp, 1973). Tapper (1973) found that whereas most female young-of-the-year dispersed in the autumn of their first year, many males did not do so until the following spring. Spring then, may be a particularly stressful period for young males, and it may be these individuals which are carrying most of the large population of trichostrongyloids. However, preliminary data of Samuel (1970) do not confirm this; prevalence in one-year-old pikas was no higher than that in older pikas.

Amount of fat storage is an index of condition. Millar (1971) weighed interscapular, cardiac, and splenic fat bodies and expressed the total as an index of fat scaled for body weight. According to this index, females are in their poorest condition from July to early August, and best in May and early June. Males are poorest in May and June, and improve in July and August. Low fat index corresponds well with high trichostrongyloid levels for both sexes.

Dunsmore (1972) suggests that burdens of *G. strigosum* in rabbits increase with increase in density of host popula-

tion and decrease in living space, both of which are stressors (Myers et al., 1971). Although the same trends existed for *T. retortaeformis*, there were no significant density or space effects.

In conclusion, the two trichostrongyloids in *O. princeps* show similar sex differences in their seasonal patterns of infection levels. In contrast to studies on trichostrongyloid population cycles in feral rabbits, which indicate the influence of reproductive hormones, this study implies that populations of trichostrongyloids in pikas increase due to poor condition of the host.

Only one other species group in *O. princeps*, *Cephaluris* spp., was significantly different in abundance between host sexes (Figure 8d). Females consistently had greater abundances of *Cephaluris* spp. than males. I am unable to offer an explanation for this; the same species pair in *O. collaris* had identical populations in males and females. Dunsmore (1966c) found the pinworm *Passaluris ambiguus* at much higher levels in female rabbits than males, but only during the breeding season.

In *O. collaris*, two species, *L. rauschi* and *E. talkeetnacuris* exhibited significant differences due to host sex, adjusted for season (Figure 8b and 8c). Unfortunately, sample sizes for collection periods were low, particularly for female hosts, and these may have biased the results. No interpretable trends are obvious with these species, so I feel that a greater sample size would be necessary before

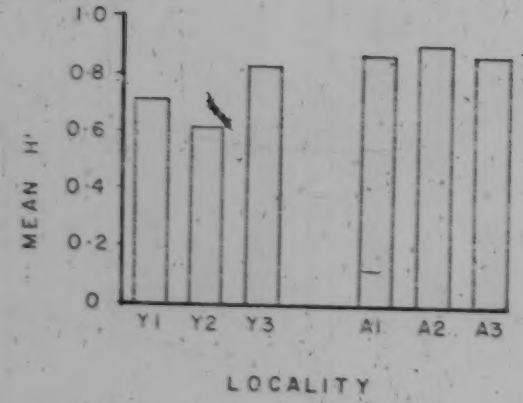
drawing any conclusions.

D. Location

Helminth communities in adult pikas, from the three collection sites in the Yukon and the three major sites in Alberta, were compared with each other by one-way analysis of variance. Shannon-Weaver diversity values (Figure 9) are not significantly different between any pair of the collection sites. Species richness however, is significantly lower in the Yukon communities compared with Alberta communities; and among the Yukon communities, site Y2 has significantly lower species richness than Y3, 10 km distant. It is tempting to postulate the existence of a control of diversity from the apparent constancy of Shannon-Weaver diversities, in contrast with the variation in species richness and species composition. However, I believe it to be a reflection of the low potential species richness and the mathematical nature of the diversity index, rather than a biological property, since the index has a maximum of ln S.

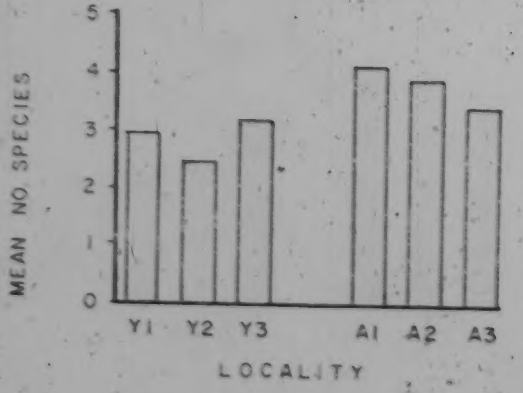
Three (*Schizorchis caballeroi* and *Cephaluris* spp.) of the five species present in the Yukon communities (Figure 10a), and one (*Murielus harpaspiculus*) of the seven in the Alberta communities (Figure 10b), differ significantly in abundance between locations. The three species in the Yukon are less abundant at site Y2 than at either of the other sites. Interestingly, fleas on these pikas show a similar relationship; prevalences of 75 and 60% were found for *Monopsyllus*

Figure 9. Mean Shannon-Weaver diversity values (H'), mean number of species, and analysis of variance for infracommunities of helminths in adult pikas from different geographical localities. See Figure 1 for locations of sites.



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	5	0·212	1·80	N.S.
ERROR	133	0·118		

SAMPLE SIZE 36 13 30 31 16 13



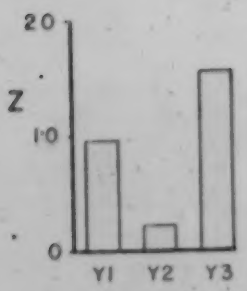
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	5	8·252	7·51	P< 0·005
ERROR	133	1·099		

Y2 Y1 Y3 A3 A2 A1

Figure 10. Abundance values (Z) for suprapopulations, and analysis of variance on $\log_{10}$ (N + 1) for infrapopulations of helminths in adult a) *Ochotona collaris* and b) *O. princeps*, from different geographical localities. See Figure 1 for location of sites.

SAMPLE SIZE 36 13 30

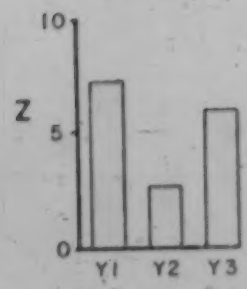
HELMINTHS IN *OCHOTONA COLLARIS*



SCHIZORCHIS CABALLEROI

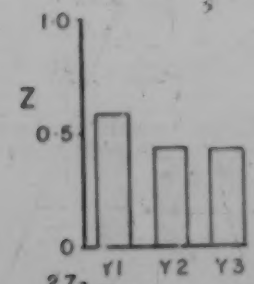
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	1·401	6·01	$P < 0.005$
ERROR	76	0·233		

Y2 Y1 Y3



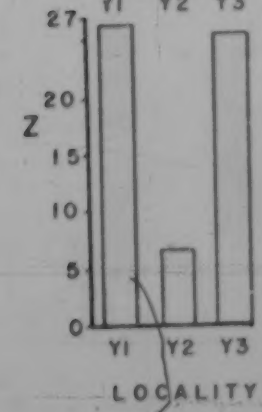
EUGENURIS TALKEETNAEURIS

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·386	1·62	N.S.
ERROR	76	0·238		



LABIOSTOMUM RAUSCHI

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·0057	0·05	N.S.
ERROR	76	0·225		



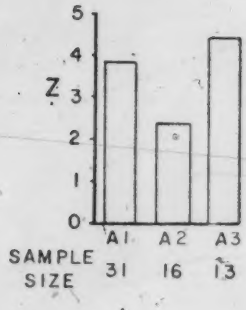
CEPHALURIS SPP.

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	2·045	9·07	$P < 0.005$
ERROR	76	0·225		

Y2 Y1 Y3

Figure 10. Continued.

HELMINTHS IN *OCHOTONA PRINCEPS*

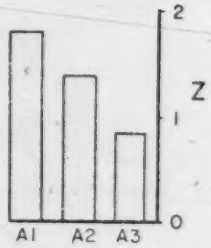


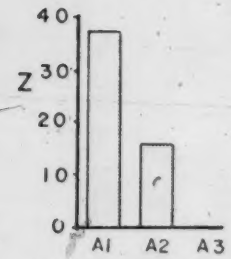
SCHIZORCHIS CABALLEROI

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·053	0·34	N. S.
ERROR	55	0·157		

GRAPHIDIELLA OCHOTONAE

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·022	0·15	N. S.
ERROR	55	0·149		

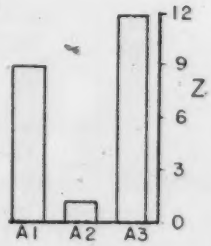




MURIELUS HARPESPICULUS

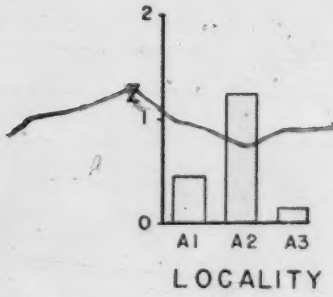
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	6·800	16·13	P<0·005
ERROR	55	0·422		

A3 A2 A1



EUGENURIS species A

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·805	2·34	N. S.
ERROR	55	0·344		

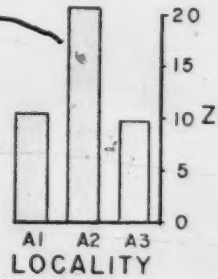


LABIOSTOMUMUM COLORADENSIS

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·222	1·88	N. S.
ERROR	55	0·118		

CEPHALURIS SPP.

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	2	0·211	0·97	N. S.
ERROR	55	0·217		



tolli at sites Y1 and Y3 respectively, but no fleas were present on pikas from site Y2 (unpublished data). In Alberta, *M. harpespiculus* is absent from site A3, but quite abundant 3 km distant at site A2.

These data support the hypothesis that pikas are grouped in semi-isolated populations. Smith (1974a, 1974b) treated pika populations as islands, and considered them to be in a dynamic equilibrium of extinction and recolonization. Extinction is inversely related to island size, and recolonization inversely related to inter-island distance (MacArthur and Wilson, 1967). Smith (1974a) considered that distances greater than 300 m were difficult barriers for dispersal by young pikas, but he was working with populations at the low altitudinal limit of the species range. He considered that high temperature limited dispersal distance (Smith, 1974b). Pikas are known to be intolerant of high temperature (MacArthur and Wang, 1973).

Tapper (1973) undertook a removal experiment to test the rate of recolonization in an area considered closer to the core of the species range. In this area (located 60 km south of my site A1 in Alberta), almost all the available habitat was filled. He removed all the pikas from an isolated slide in May, and observed the area every two weeks for sign of pikas. Prior to removal, an average population of eight adults resided on the slide. In August, a juvenile male previously seen on a slide 3 km distant, appeared on the slide, and took up residence. However, by the following year, he

was still alone. When pikas were removed from another less isolated area, only 200-300 m from the closest pikas, the experimental area became saturated again only two months later. Thus in Alberta, pikas can potentially disperse over relatively long distances.

My data on parasites indicate that few dispersing pikas become established on occupied habitat. The extreme example is with *M. harpespiculus* in Alberta, where two of the collection sites with radically different abundances, A2 and A3, are only 3 km distant, and not obviously separated by a barrier. This indicates that even in the core of the species range, *O. princeps* (and *O. collaris*) populations and their helminth suprapopulations, may be regarded as islandic. If this is so, then local extinctions of helminth populations such as that of *M. harpespiculus* are not unexpected. One would expect a much greater rate of extinction with helminth suprapopulations than with host populations, because each host individual is itself an island, which may or may not contain an infrapopulation of helminths.

Site Y2, where species richness and abundance of two species of helminths and of the flea *M. tolli*, are consistently lower, may represent recent recovery from a local host population extinction. However, considering the large size of this population, its proximity to other populations, and that all the available habitat in the entire region appeared to be filled (personal observation), this seems intuitively unlikely. Instead this area may have suffered more local

extinctions of helminth suprapopulations than the other areas. Although large, this population of pikas seems smaller and more isolated than the other two sampled in the Yukon, which could explain the higher rate of extinction. Another explanation could be that the area provides marginal habitat for the larval stages of these parasites.

E. Age

Samuel (1970) provided preliminary evidence that there are no differences in prevalence between helminth suprapopulations in different age classes of adult *O. princeps*. His data also indicate a gradual acquisition of helminths by juvenile pikas over their first summer. I analyzed additional data on sequence and rate of acquisition of helminths by juveniles but not by adults.

To obtain groups of hosts comparable in size between juvenile age classes of the two species of pikas, I placed individuals in one of three groups for each host species (designated a-c), as shown in Figure 11. The groups are only approximately equivalent in host age between host species.

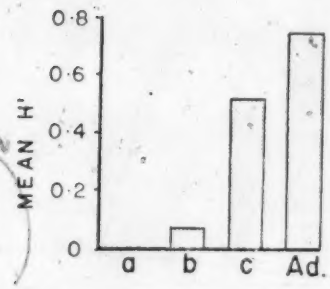
Similar trends in diversity and species richness are apparent in the development of supracommunities in both host species (Figure 11). By age c (approximately 55 days), communities are similar in diversity and species richness to communities in adult pikas. This is a rather rapid development, since no pika younger than 44 days for *O. collaris*, or 39 days for *O. princeps*, was infected.

Figure 11. Mean Shannon-Weaver diversity values (H'), number of species, and analysis of variance for infracommunities of helminths in pikas of different ages. The ages of each group are as follows:

Ochotona collaris: a) 21-39 days
b) 44 days
c) 65 days
Ad.) Adult

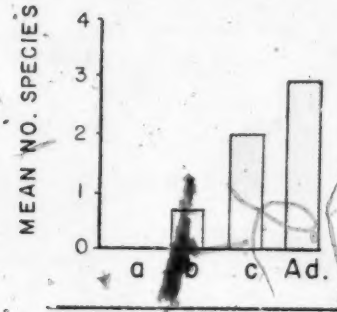
Ochotona princeps: a) 14-38 days
b) 39-50 days
c) 52-65 days
Ad.) Adult

n= 6 3 4 79 COMMUNITIES IN *OCHOTONA COLLARIS*



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	1·434	12·05	P<0·005
ERROR	88	0·119		

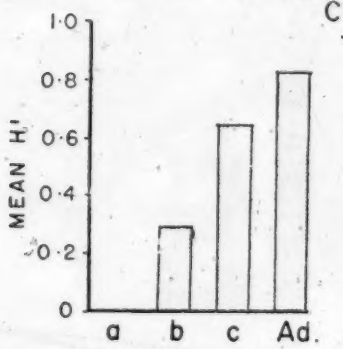
a b c Ad.



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	20·695	22·39	P< 0·005
ERROR	88	0·924		

a b c Ad.

n= 12 5 6 79 COMMUNITIES IN *OCHOTONA PRINCEPS*



SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	2·645	26·10	P<0·005
ERROR	98	0·101		

a b c Ad.

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	54·370	44·05	P< 0·005
ERROR	98	1·233		

a b c Ad.

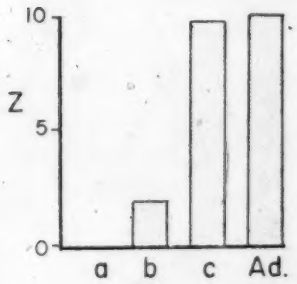
The earliest invader in *O. collaris* (Figure 12a) is *Schizorchis caballeroi*. *Cephaluris* spp. are present early, but are not as abundant in juveniles as in adults. *Eugenuris talkeetnaeuris* reaches abundance characteristic of adult pikas by age c, but still appears to be a late invader. *Labiostomum rauschi* is consistently in low abundance, and is impossible to analyze given the present sample sizes, but it appears to be a late invader.

In *O. princeps* (Figure 12b), *S. caballeroi* again is an early invader, but *Graphidiella ochotonae* and *Murielus harpespiculus* reach abundances characteristic of adult pikas earlier. The pinworms are somewhat slower in invading. *Labiostomum coloradensis* is always in low abundance, so is difficult to analyze. *Eugenuris* sp. A and *Cephaluris* spp. are relatively late invaders, although they reach abundances chatacteristic of adults by age c.

Pikas begin to emerge from the nest about 21 days after birth, and are weaned at 21-28 days (see Chapter IV). It is surprising that helminth infections do not occur until another 10-15 days have elapsed. Unpublished data acquired as an offshoot of work by Hobbs and Samuel (1974), show that pikas acquire coccidian (Protozoa: Eimeriidae) infections much earlier than helminth infections. Coccidia have direct life cycles, as do all the helminths encountered here except *S. caballeroi*. One pika (*O. princeps*) was passing more than 10,000 oocysts of *Eimeria circumborealis* per gram of faeces at 17 days of age, presumably before weaning. The difference

Figure 12. Abundance values (Z) for suprapopulations, and analysis of variance on $\log_{10}$ (N + 1) for infrapopulations of helminths in a) *Ochotona collaris* and b) *O. princeps* of different ages. The ages of each group are as in Figure 11.

12 A HELMINTHS IN *OCHOTONA COLLARIS*



SCHIZORCHIS CABALLEROI

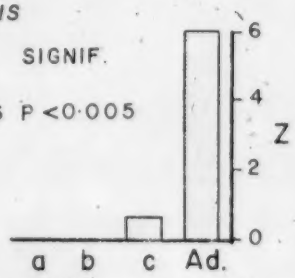
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	1·330	5·13	P<0·005
ERROR	88	0·259		

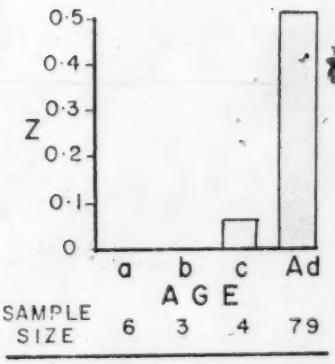
a b Ad. c

EUGENURIS TALKEETNAEURIS

SOURCE	D.F	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	1·324	6·06	P<0·005
ERROR	88	0·218		

a b c Ad.





LABIOSTOMUM RAUSCHI

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	0·151	1·57	N.S.
ERROR	88	0·096		

CEPHALURIS SPP.

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	3·861	14·92	P< 0·005
ERROR	88	0·259		

a b c Ad.

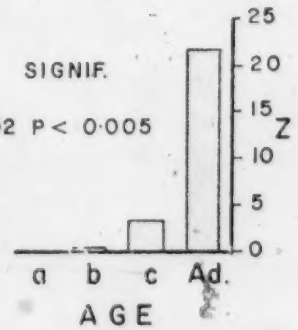
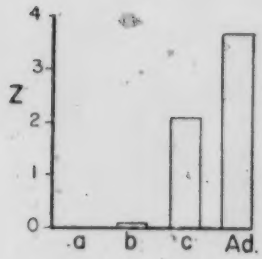


Figure 12. Continued.

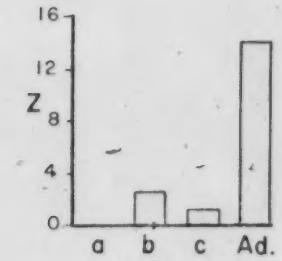
12 B HELMINTHS IN *OCHOTONA PRINCEPS*



SCHIZORCHIS CABALLEROI

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	1·426	10·74	P < 0·005
ERROR	98	0·133		

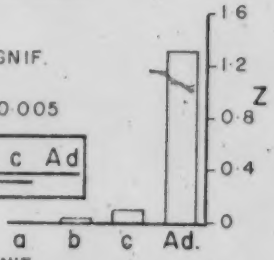
a b c Ad



GRAPHIDIELLA OCHOTONAE

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	0·548	4·33	P < 0·005
ERROR	98	0·127		

a b c Ad



MURIELUS HARPE SPICULUS

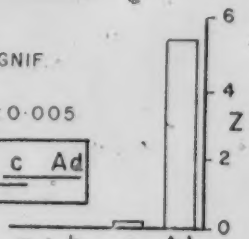
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	2·357	4·43	P < 0·025
ERROR	98	0·532		

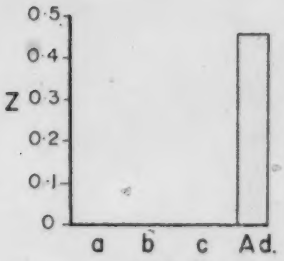
a c b Ad

EUGENURIS species A

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	1·378	5·42	P < 0·005
ERROR	98	0·254		

a b c Ad





SAMPLE SIZE 12 5 6 79

LABIOSTOMUM COLORADENSIS

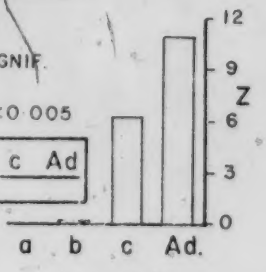
SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	0·243	2·65	P < 0·05
ERROR	98	0·092		

a b c Ad

CEPHALURIS SPP.

SOURCE	D.F.	MEAN SQUARE	F	SIGNIF.
TREATMENT	3	3·397	16·80	P < 0·005
ERROR	98	0·202		

a b c Ad



between time of acquisition of helminths and coccidia could be caused by the following:

(i) helminths have a longer development time in pikas than do coccidia and are not detected until later

(ii) pikas do not encounter infective stages of helminths as early as they encounter sporulated (= infective) coccidia oocysts

(iii) young pikas are refractory to infection with helminths, but not to coccidia.

With the exception of sporulation times of some coccidia, life-cycles or development times of helminths or coccidians in pikas are unknown. However, related species of each group are not as divergent in development time as would be required for the first explanation. For example, *Aspiculuris tetraptera*, a relative of pika pinworms, has no mucosal stage, the development being entirely lumenal (Philpot, 1924), and worms are detectable in the caecum by 18 hours post-infection. Oocysts of *Eimeria perforans* are present in the faeces of rabbits (*Oryctolagus cuniculus*), six days post-infection (Kheysin, 1967).

It is likely that unweaned pikas eat the faeces of the female parent, as has been suggested for jackrabbits (*Lepus californicus*) in California (Lechleitner, 1957). If coccidian oocysts in the faeces sporulate more quickly than nematode eggs develop to infectivity, juvenile pikas could be exposed to the former and not the latter. Oocysts of *Isospora marquardti*, *Eimeria banffensis*, *E. cryptobarretti*, *E. princepsis*, and *E. calantinei*, all coccidians of pikas, sporu-

lated within 72 hours at 30°C (Duszynski and Brunson, 1972, 1973). Eggs of *Aspiculuris tetraptera* become infective in 6-7 days (Anya, 1966).

The third explanation is also probable in view of the late acquisition, but subsequent rapid development of helminth communities, but cannot be supported without experimental evidence. It could be mediated directly by the host in terms of necessary conditions for individual helminth species to develop, or via interactions with other species, as a successional phenomenon.

There is not enough known of the biology of any pika helminths to explain why individuals of *S. caballeroi*, *G. ochotonae* or *M. harpespiculus* invade younger pikas than the pinworms are able to invade. The possibilities discussed above in relation to coccidian infections, may apply equally well to differences in acquisition rates between helminth species.

F. Clumped Infective Stages

Although I have no quantitative information on this topic, no doubt much of the cause for over-dispersion of helminths in pikas is due to the clumping of infective stages. Eggs are passed in the faeces, which are eliminated as discrete pellets. Groups of these pellets are clumped into faecal piles because a pika tends to defaecate at a limited number of locations within its territory.

For the direct life-cycle helminths, including all the

nematodes, a pika coming into contact with one infective individual increases its probability of contact with others. The situation is not as simple with *S. caballeroi*. Other anoplocephalines for which life cycles are known, use oribatid soil mites as intermediate hosts (Kates, 1965). For clumping to occur here, either the mites have a clumped distribution, or the cysticercoids are distributed non-randomly in mites. One very likely area of contact between pikas and soil mites is the hay pile. A well developed soil accumulates at hay pile sites, since the same sites may be used year after year.

CHAPTER VII

ECOLOGY: INTERACTIONS

A. Introduction

Interspecific interactions occur among parasites living in the same host (Leigh-Sharpe, 1933; Cross, 1934; for more examples see Holmes, 1973). Holmes (1961, 1962) provided experimental evidence in a classical study of competition between the cestode *Hymenolepis diminuta* and the acanthocephalan *Moniliformis dubius* in laboratory rats.

Interactions between parasites may take many forms, including competitive exclusion, inhibition of maturation or growth, and site displacement. In competitive exclusion, one of the earliest forms to be demonstrated, the number of one species is reduced in hosts infected with a second (see Holmes, 1973 for examples). Schad (1966) regarded cross-immunity as an indirect form of competitive exclusion. The converse of competitive exclusion, interactive enhancement, has received little attention, but there are examples (Ewing and Todd, 1961a, 1961b; Thomas, 1964; Cloutman, 1975).

Although there are many examples of intraspecific inhibition of maturation (Avery, 1969; Ghazal and Avery, 1974), very few examples of interspecific inhibition of maturation have been observed. Holmes (1962) suggested that

the presence of *M. dubius* reduced the egg output of *H. diminuta* in rats. Leong (1975) presented evidence that the proportion of gravid females of the acanthocephalan *Metechinorhynchus salmonis* in lake trout (*Salvelinus namaycush*) is inversely proportional to the number of cestode individuals (*Eubothrium salvelini*). An interactive size reduction effect, similar to the well known intraspecific "crowding effect" (Chandler, 1939), has been demonstrated for *M. dubius* and *H. diminuta* (Holmes, 1962).

According to Holmes' (1973) scheme, organisms may avoid competition of the above kinds by interactive site segregation. The best known example in helminths is the displacement of *H. diminuta* by *M. dubius* (Holmes, 1961, 1962); a few other examples are given by Holmes (1973). Many more examples of selective site segregation have been observed (see Holmes, 1973; and Crompton 1973 for reviews). Holmes (1973) suggests that selective site segregation is the probable evolutionary outcome of interactive site segregation, and postulates that the reason for the relative paucity of cases of interactive site segregation is that most parasite communities are not young.

Helminth communities in pikas afford several examples of interspecific interaction and site selection. I will discuss examples of competitive exclusion or interactive enhancement first, then interactive site segregation, and selective site segregation.

B. Competitive Exclusion and Interactive Enhancement

A simple method of testing for competitive exclusion is to compare the frequencies of occurrence of each species of all possible pairs of species, in single and concurrent infections. This was done with 2 x 2 Chi-squared contingency tests (Steel and Torrie, 1960, p. 371). Juvenile pikas were excluded from these tests, since so few were infected with helminths; their inclusion would have biased the outcome toward positive interaction.

Not one of these tests indicated a significant (i.e., $p \leq 0.05$) competitive exclusion between species (Figure 13), but four species-pairs were found concurrently more often than by chance. Two others, both involving the two genera *Labiostomum* and *Cephaluris*, were strongly indicative of positive interaction, but were not statistically significant ($p < 0.1$ for each). In each comparison, *Labiostomum* was found only in pikas concurrently infected with *Cephaluris*.

Rank correlation is another method of detecting competitive exclusion. It is a little more sensitive than 2 x 2 contingency tests, because it allows for those situations in which competitive exclusion is not absolute; that is, large numbers of species A reduce the numbers of B without completely excluding B. Rank correlations were determining for only those pikas which were infected with at least one species of the pair. Once again, no statistically significant cases of negative interactions were detected with Spearman's rank correlation (Steel and Torrie, 1960, p. 409).

Figure 13. Trellis matrix of 2 x 2 contingency tables for all possible pairs of species. The Chi-square value is given below each box. All interactions are not significant, except those marked *($p < 0.05$), **($p < 0.01$), or ***($p < 0.005$).

COMMUNITIES IN *CCHOTONA PRINCEPS* (N = 88)

		+	−
GRAPHIDIELLA OCHOTONAE	+	39	11
	−	31	7

0·170

		+	−
MURIELUS HARPESPICULUS	+	38	8
	−	32	10

0·556

		+	−
MURIELUS HARPESPICULUS	+	28	18
	−	22	20

0·645

		+	−
EUGENURIS species A	+	44	10
	−	26	8

0·332

		+	−
EUGENURIS species A	+	30	24
	−	20	14

0·091

		+	−
EUGENURIS species A	+	28	26
	−	18	16

0·010

		+	−
LABIOSTOMUM COLORADENSIS	+	20	8
	−	50	10

1·663

		+	−
LABIOSTOMUM COLORADENSIS	+	17	11
	−	33	27

0·254

		+	−
LABIOSTOMUM COLORADENSIS	+	16	12
	−	30	30

0·390

		+	−
LABIOSTOMUM COLORADENSIS	+	23	5
	−	31	29

7·479**

		+	−
CEPHALURIS SPP.	+	63	18
	−	7	0

1·956

		+	−
CEPHALURIS SPP.	+	45	36
	−	5	2

0·662

		+	−
CEPHALURIS SPP.	+	43	38
	−	3	4

0·270

		+	−
CEPHALURIS SPP.	+	50	31
	−	4	3

0·057

		+	−
CEPHALURIS SPP.	+	28	53
	−	0	7

3·549

SCHIZORCHIS CABALLEROI — GRAPHIDIELLA OCHOTONAE — MURIELUS HARPESPICULUS — EUGENURIS species A — LABIOSTOMUM COLORADENSIS

COMMUNITIES IN *OCHOTONA COLLARIS* (N = 79)

		+	−
EUGENURIS TALKEETNAEURIS	+	54	9
	−	13	3

0·197

		+	−
LABIOSTOMUM RAUSCHI	+	25	4
	−	42	8

0·069

		+	−
LABIOSTOMUM RAUSCHI	+	27	2
	−	36	14

5·061*

		+	−
CEPHALURIS SPP.	+	64	9
	−	3	3

6·108*

		+	−
CEPHALURIS SPP.	+	63	10
	−	0	6

25·57***

		+	−
CEPHALURIS SPP.	+	29	44
	−	0	6

3·766

SCHIZORCHIS CABALLEROI — EUGENURIS TALKEETNAEURIS — LABIOSTOMUM RAUSCHI

Positive correlations were found between some of the pinworm pairs (Figure 14).

Most of the instances of positive interactions involved pairs of pinworms. According to Gause's competitive exclusion principle, one might expect strong negative interactions between such closely related species. The question then arises how these species co-exist. Following the evolutionary sequence of Holmes (1973, figure 2), one would predict these species to be segregating resources, either interactively or selectively, such that competition is reduced; this is often so (see below).

With resource segregation however, one would still expect only a lack of competitive exclusion, not an interactive enhancement. Occurrence of the latter among pinworms, might be due to similarities in life-cycle and development outside the host, so that the helminths are more common in individual pikas which inhabit areas of particularly good habitat for the free-living stages of all the pinworms.

Ewing and Todd (1961a, 1961b) demonstrated experimentally, an association between two species of lungworms *Metastrongylus apri* and *M. pudentotectus*, in swine. When infective stages of these helminths were administered concurrently, the number reaching maturity was much greater for both species than when administered singly, even though there was no apparent site segregation.

Colwell and Wescott (1973) showed experimentally that a mouse-adapted strain of *Nippostrongylus brasiliensis* bene-

Figure 14. Trellis matrix of results of Spearman's rank correlation (SRC) of intensity for all possible pairs of species. Values in each box are explained in the key.

COMMUNITIES IN *OCHOTONA PRINCEPS*

	SCHIZORCHIS CABALLEROI	GRAPHIDIELLA OCHOTONAE	MURIELUS HARPESPICULUS	EUGENURIS species A	LABIOSTOMUM COLORADENSIS
GRAPHIDIELLA OCHOTONAE	−0·016 86 N.S.				
MURIELUS HARPESPICULUS	+0·035 86 N.S.	+0·090 75 N.S.			
EUGENURIS species A	−0·011 85 N.S.	−0·179 78 N.S.	−0·138 79 N.S.		
LABIOSTOMUM COLORADENSIS	−0·075 82 N.S.	−0·172 63 N.S.	−0·148 65 N.S.	+0·015 60 N.S.	
CEPHALURIS SPP.	−0·035 95 N.S.	+0·012 93 N.S.	−0·044 93 N.S.	+0·283 90 P<0·01	+0·549 86 P<0·01

KEY

SRC COEFF.
SAMPLE SIZE
SIGNIFICANCE

COMMUNITIES IN *OCHOTONA COLLARIS*

	SCHIZORCHIS CABALLEROI	EUGENURIS TALKEETNAEURIS	LABIOSTOMUM RAUSCHI
EUGENURIS TALKEETNAEURIS	+0·124 80 N.S.		
LABIOSTOMUM RAUSCHI	−0·071 74 N.S.	+0·219 67 N.S.	
CEPHALURIS SPP.	−0·044 79 N.S.	+0·417 76 P<0·01	+0·277 75 P<0·01

fitted from concurrent infection with *Nematospiroides dubius*. Whereas *N. brasiliensis* is eliminated after 12 days by an immune reaction in single-species infections, worms are still present at 60 days in concurrent infections. There is apparently no effect of *N. brasiliensis* on *N. dubius* infections. In a further series of experiments including host-to-host transfers, Jenkins (1975) showed that only those worms which have developed in mice infected with, or previously exposed to *N. dubius*, have a prolonged longevity. He postulated that worms became adapted during their larval stage, to antibodies developed against *N. dubius*.

Positive interactions have been observed in field studies, but can often be attributed to mutual requirements at the infective stage, and similarities in life-cycle. Thomas (1964) recorded positive relationships between helminth species in brown trout, which he attributed to feeding preferences of the hosts, and Cloutman (1975) reported positive relationships between gill parasites of bass, warmouth and bluegill.

Kisielewska (1970d) reported some interesting examples of positive relationships of helminths in the vole *Clethrionomys glareolus*. She found three positive relationships, all between species occurring in different sites in the host. I re-analyzed her data for two of these associations with 2 x 2 Chi-square contingency tests, and found only one (*Heligmosomum halli* and *Catenotaenia pusilla*) to be statistically ($p \leq 0.05$) significant. Kisielewska (1970d) also

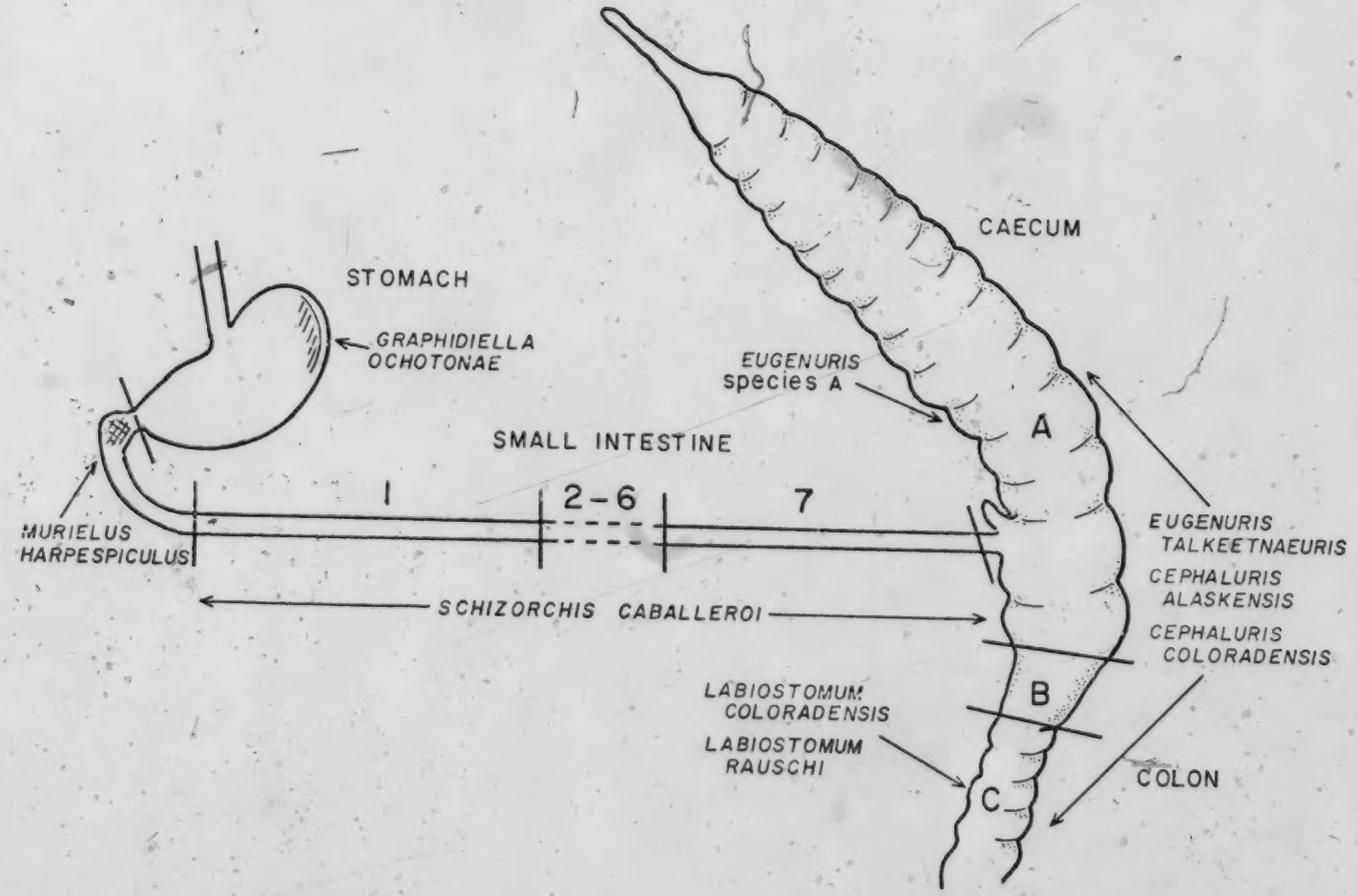
claimed that while there was a positive interaction for co-occurrence of *H. halli* and *C. pusilla*, there was a negative relationship between intensity of infection of the two species. The figure she refers to for evidence however (Kisielewska's 1970d, figure 2), does not show any such relationship. Her reasoning requires the assumption of a random distribution of intensity frequencies in single-species infections, a situation she did not encounter except in species with very low prevalence (Kisielewska, 1970c, 1970d). Sample 2 x r Chi-square analyses I ran, using data from her figure (1970d, figure 2), between intensity frequency distributions of one species under differing intensities of the other, showed no significant effects.

The positive relationships found between pinworm species of pikas in this study could be explained as being caused by similarity in life-cycle. An experimental study is required to test for more direct relationships between species. Such an approach may prove fruitful for the effect of other species of pinworms on the establishment of *L. rauschi* and *L. coloradensis*. No individuals of these species were present in pikas which were not infected with *Cephaluris* spp. (Figure 13), hinting to the possibility of a successional phenomenon.

C. Interactive Site Segregation

Figure 15 indicates the sites at which helminths of each species are found. Only the pinworms overlap in distri-

Figure 15. Diagrammatic view of the gastro-intestinal tract of a pika, showing the sites occupied by helminths encountered in this study.


CAECUM
STOMACH
GRAPHIDIELLA OCHOTONAE
EUGENURIS species A
SMALL INTESTINE
A
1
2-6
7
MURIELUS HARPESPICULUS
EUGENURIS TALKEETNAEURIS
CEPHALURIS ALASKENSIS
SCHIZORCHIS CABALLEROI
CEPHALURIS COLORADENSIS
B
LABIOSTOMUM COLORADENSIS
LABIOSTOMUM RAUSCHI
COLON
C

butions; more will be said of these later.

In order to test for interactive site segregation of the two small intestinal worms, *Murielus harpespiculus* and *Schizorchis caballeroi*, the small intestine was physically partitioned into approximately eight sections immediately after the host's death, by tying off with cotton thread. The anterior-most section was only about 3-4 cm in length, while the remaining seven were approximately 15 cm. Some intestines were partitioned into more or less than eight sections in the field, and were standardized to eight for the analyses. Thus, each section is represented by a different sample size of hosts. To compensate for this, a form of prevalence measure was used, in terms of the frequency of infection in each of the sections. The mean number of worms per section (including uninfected sections) was also calculated. Results are shown in Figure 16. Only those pikas which were infected with *S. caballeroi* were included in the analyses.

The heligmosome *M. harpespiculus* is an extreme habitat specialist and occurs almost exclusively in the anterior duodenum, within about 5 mm of the pyloric sphincter (Figure 15). The cestode *S. caballeroi*, was not found in this region and is a habitat generalist inhabiting the remainder of the small intestine. For the analysis, *M. harpespiculus* intensities were divided into three classes: absent, low (1-10, mean 4.6 worms), and high (11-186, mean 69). *Schizorchis caballeroi* was categorized by size as: small (up to about

Figure 16. Intestinal distribution of small and large *Schizorchis caballeroi* in pikas with different levels of concurrent infection with *Murielus harpespiculus*. a) Intensity, and b) prevalence. Locations of sections 1-7 are shown in Figure 15.

S. caballeroi in *O. collaris*, not infected with *M. harpespiculus* (n: 52 pikas).

S. caballeroi in *O. princeps*, not infected with *M. harpespiculus* (n: 15 pikas).

S. caballeroi in *O. princeps*, infected with 1-10 *M. harpespiculus* (n: 10 pikas).

S. caballeroi in *O. princeps*, infected with 11-186 *M. harpespiculus* (n: 18 pikas).

16 A PREVALENCE

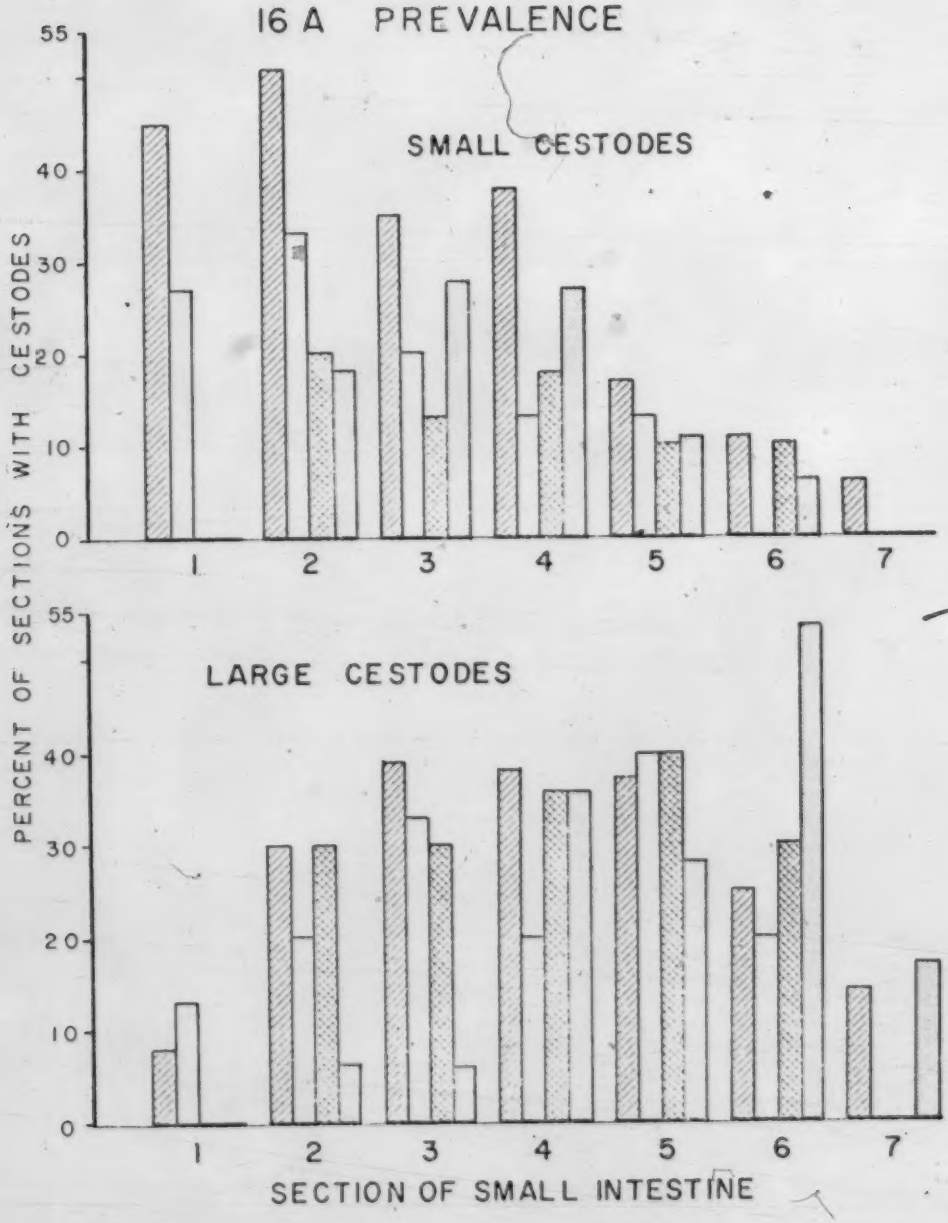


Figure 16. Continued.

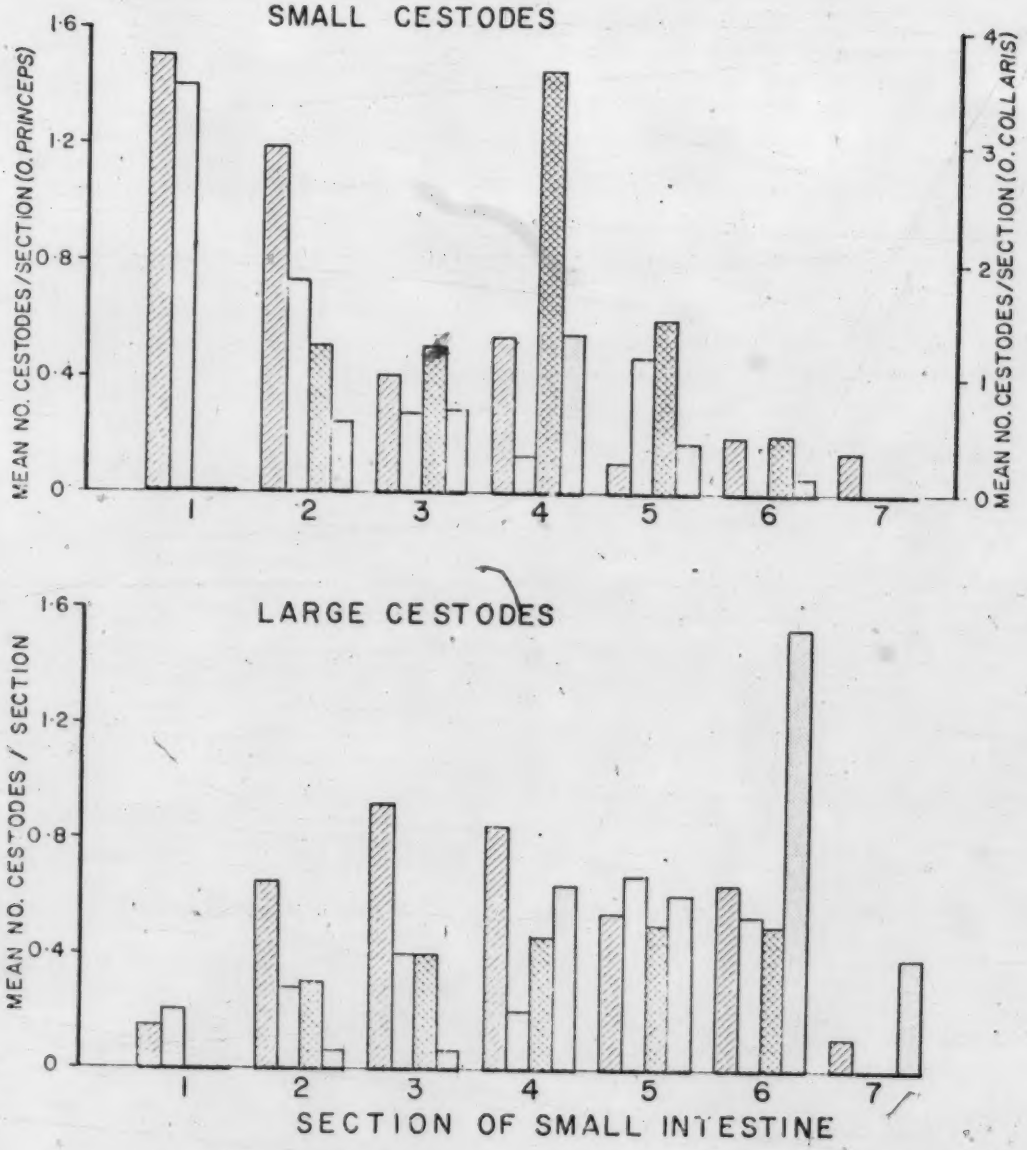
S. caballeroi in *O. collaris*, not infected with *M. harpespiculus* (n: 52 pikas).

S. caballeroi in *O. princeps*, not infected with *M. harpespiculus* (n: 15 pikas).

S. caballeroi in *O. princeps*, infected with 1-10 *M. harpespiculus* (n: 10 pikas).

S. caballeroi in *O. princeps*, infected with 11-186 *M. harpespiculus* (n: 18 pikas).

16 B INTENSITY



4 mm), or large (4-40 mm). It is uncertain whether or not the small worms represent new infections.

Distributions of *S. caballeroi* under different *M. harpespiculus* intensity classes are shown in Figure 16. Differences between prevalence distributions (Figure 16a) were tested using a three-way G-test (Sokal and Rohlf, 1969, p. 601), and intensity distributions (Figure 16b) by a two-way G-test (Sokal and Rohlf, 1969, p. 509); the results are presented in Table 15.

Although the distributions of each of the two species in single species infections do not overlap, in concurrent infections *S. caballeroi* is displaced towards the posterior end of the small intestine. High heligmosome infrapopulations have a significant effect on both large and small cestodes. Low heligmosome infrapopulations do not have a significant effect on the distribution of large cestodes, but are as effective as high populations in altering the intensity distribution of small cestodes.

In the well-known interaction of *Moniliformis dubius* and *Hymenolepis diminuta* in rats (Holmes, 1961), the specialist (*M. dubius*) shifts the distribution of the generalist. The system in pikas is similar except that the normal habitat ranges do not overlap. It is unlikely that the two species are competing for a resource, and particularly unlikely that *S. caballeroi* could deplete a resource of *M. harpespiculus*, since the latter is upstream. Consequently, there may be no functional significance to the shift. There is another,

Table 15. Results of statistical comparisons (G-tests) between distributions of *Schizorchis caballeroi* along the small intestines of *Ochotona* spp., under different levels of concurrent infection with *Murielus harpespiculus*

	"Prevalence"		"Intensity"	
Test	G-value*	Signif.	G-value*	Signif.
Large cestodes				
Y vs A_0	4.56	$p > 0.5$	9.58	$p > 0.1$
(Y,A_0) vs A_{1-10}	3.59	$p > 0.5$	1.20	$p > 0.95$
(Y,A_0) vs A_{11+}	22.35	$p < 0.005$	51.38	$p < 0.005$
Small cestodes				
Y vs A_0	4.46	$p > 0.5$	16.01	$p < 0.025$
(Y,A_0) vs A_{1-10}	7.00	$p > 0.25$	--	--
(Y,A_0) vs A_{11+}	14.44	$p < 0.025$	--	--
A_0 vs A_{1-10}	--	--	33.96	$p < 0.005$
A_0 vs A_{11+}	--	--	26.46	$p < 0.005$
.....				
Large (Y,A_0) vs Small (Y,A_0)	40.13	$p < 0.005$	204.46	$p < 0.005$

* df = 6, in all cases.

Y Distributions of *S. caballeroi* in *O. collaris* from Yukon.

A_0 Distributions of *S. caballeroi* in *O. princeps* from Alberta, not concurrently infected with *M. harpespiculus*.

A_{1-10} Distributions of *S. caballeroi* in *O. princeps* from Alberta, concurrently infected with from 1 to 10 *M. harpespiculus*.

A_{11+} Distributions of *S. caballeroi* in *O. princeps* from Alberta, concurrently infected with 11 or more *M. harpespiculus*.

though somewhat less convincing, reason for discounting resource competition as a reason. Chappell et al. (1970) observed an anterad migration of *H. diminuta* in rats, in response to suboptimal host diets. One would thus expect *S. caballeroi* to be found more anterad if *M. harpespiculus* were depleting a food resource.

The more common general case of competition involving a specialist and a generalist is niche inclusion, where the niche of the specialist, measured along a resource gradient, is included within the potential niche of the generalist. Competition between such species is theorized to be largely by interference (Case and Gilpin, 1974). Many examples between closely related species of birds, mammals, fishes, and arthropods are given by Morse (1974) and Colwell and Fuentes (1975), in which the specialist employs interference competition against the generalist. Although the example in pikas is not niche inclusion, it appears that competition here is interference by the specialist, against the generalist. Mechanisms of interference available to parasites may be direct, or indirect via an effect on the host.

D. Selective Site Segregation

Perhaps the greatest single reason for the absence of competitive exclusion in pika helminth infracommunities is the high degree of selective site segregation shown by them. The trichostrongyloids *Graphidiella ochotonae* and *Murielus harpespiculus* are extreme specialists (Figure 15), and al-

though *Schizorchis caballeroi* is a generalist, it does not overlap with any other species.

The distribution of *S. caballeroi* requires further elaboration. It is of interest that small cestodes are situated more anterad than large ones (Figure 16, Table 15), suggesting a posterior emigration with age. There have been few reports of emigrations in this direction (Crompton, 1973: 48). Rendtorff (1948) showed experimentally that in mice, individuals of the anoplocephalid *Atriotaenia symmetrica* (Baylis 1927) Stunkard 1961, shift posterad with age. To my knowledge, my data on the intestinal distribution of *S. caballeroi* constitute the only other information of this type for an anoplocephalid.

Interpretation of the posterior migration as age related is somewhat tenuous however, because small worms are not necessarily young (Crompton, 1973, p. 48). Small and immature worms may be that way as a consequence of a crowding phenomenon (Roberts, 1961), or perhaps have destrobilated due to some other unknown cause. This problem can only be solved experimentally.

The pinworms in pikas, unlike the above species, appear to overlap considerably in their site preference (Figure 15). In order to test the degree of specialization of the pinworms within the caecum and large intestine, three natural zones were partitioned by tying with cotton thread immediately after death of the pika. These zones are shown in Figure 15. Each zone has a different internal structure (see Puget and

Voisin, 1973 for a description of the caecum and large intestine of *O. rufescens*). Zone A, consisting of the caecum and a short (10-15 mm) section of large intestine, is thin-walled and has a spiral flap throughout its length, from which extend flat fingerlike processes. The processes are progressively shorter toward the blind end of the caecum. Successive coils of this flap are approximately 5 mm apart. Zone B (= procolon of Kelsall, 1942) is short (15-25 mm), relatively thick-walled and muscular, with reticular muscle bands. Zone C is thick-walled, glandular, and is folded into three longitudinal lines of transverse pocket-like flaps or haustra.

Pikas, like other lagomorphs, are coprophagous, and excrete two distinctly different kinds of faeces. Soft faeces are loose, have a high water content, are relatively roughage-free, and have the consistency of toothpaste. Soft faeces are reingested by pikas (Johnson and Maxell, 1966; Tyndale-Biscoe, 1959) as in other lagomorphs (Bookhout, 1959; Kirkpatrick, 1956; Madsen, 1939). Hard faeces are spherical pellets, about 3 mm in diameter. They have a relatively large amount of roughage. Prospective hard faeces remain moist and do not form pellets until after passing through Zone C, but because of the relatively large amount of roughage, are easily distinguishable from soft faeces in this zone. The kind of lumen contents in Zone C, and the number of individuals of each pinworm species in each of the zones were recorded at necropsy. Preliminary result have

been published (Holmes, 1973); detailed results are shown in Figure 17.

Most specimens of *Eugenuris* species A are found in Zone A in *O. princeps* (Figure 17a), regardless of the lumen contents in Zone C. *Cephaluris* spp. had to be considered together because females were indistinguishable (see p. 30). When Zone C contained prospective hard faeces, individuals of *Cephaluris* spp. were distributed almost evenly in both A and C, with very few in B. When Zone C contained prospective soft faeces, most individuals of *Cephaluris* spp. were in Zone A. *Labiostomum coloradensis* were found almost exclusively in Zone C, regardless of the contents.

In *O. collaris* (Figure 17b), *Cephaluris* spp. and *Labiostomum rauschi* had patterns of distribution similar to their congeners in *O. princeps*. Thus, *Cephaluris* spp. were present in Zones A and C when hard faeces were forming in Zone C, and mostly in Zone A when soft faeces were forming in Zone C. Patterns of *Eugenuris talkeetnaeuris* distribution were unlike those of *Eugenuris* species A but similar to *Cephaluris* spp. patterns. Males of *Cephaluris alaskensis* and *C. coloradensis* in *O. collaris* were treated separately (Figure 17c) to determine if they were segregating, but no differences were found between them.

In summary, two species are site specific in *O. princeps* and show very little overlap: *Eugenuris* species A selects Zone A and *L. coloradensis* selects Zone C. *Cephaluris* spp. are migrators and tend to either avoid prospective soft

Figure 17. Distribution of pinworms in the three zones (A-C, see Figure 15) of the caecum and large intestine of pikas during periods of hard faeces, and soft faeces formation. Sample sizes of pinworms (and hosts) are shown below each pie. a) pinworms in *Ochotona princeps*, b) pinworms in *O. collaris*, and c) male *Cephaluris alaskensis* and *C. coloradensis* in *O. collaris*.

17A. *OCHOTONA PRINCEPS*

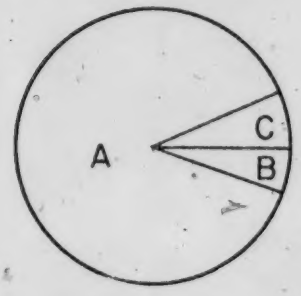
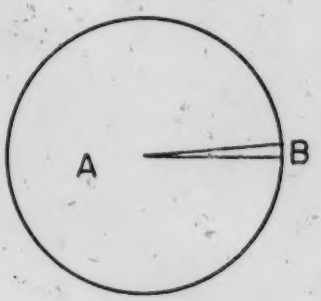
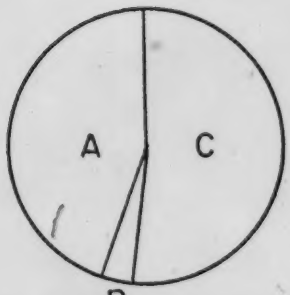
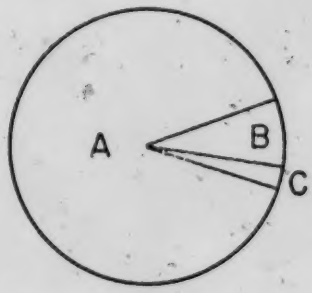
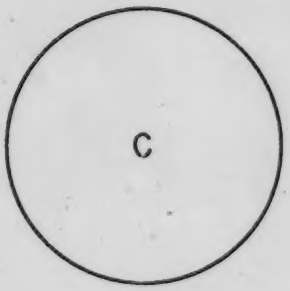
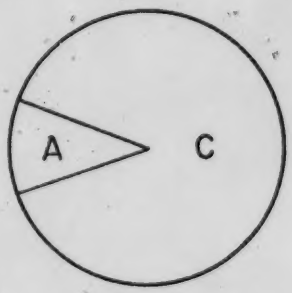
	HARD	SOFT
EUGENURIS species A	 215 (23)	 198 (9)
CEPHALURIS SPP.	 395 (34)	 200 (12)
LABIOSTOMUM COLORADENSIS	 62 (12)	 25 (4)

Figure 17. Continued.

17 B. *OCHOTONA COLLARIS*

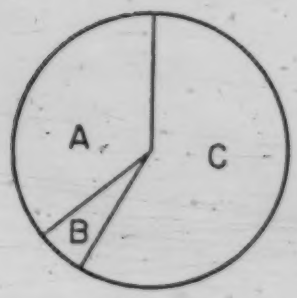
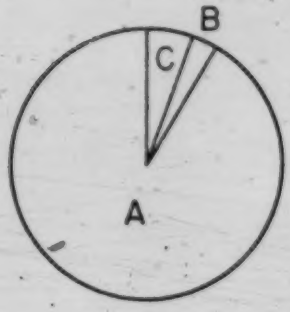
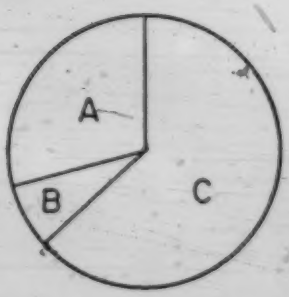
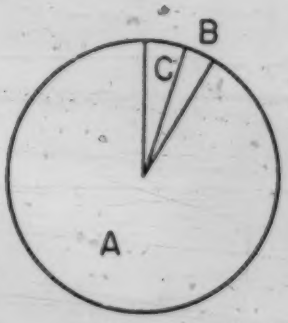
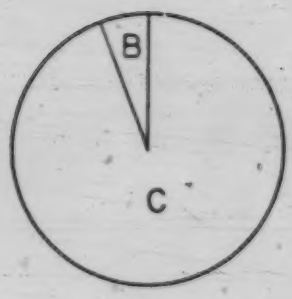
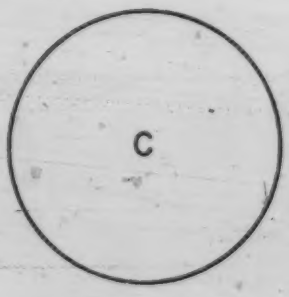
	HARD	SOFT
EUGENURIS TALKEETNAEURIS	 99 (15)	 70 (8)
CEPHALURIS SPP.	 414 (17)	 191 (8)
LABIOSTOMUM RAUSCHI	 18 (7)	 18 (3)

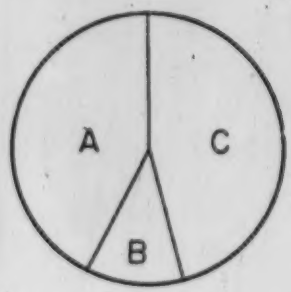
Figure 17. Continued.

17 C. *OCHOTONA COLLARIS*

MALE. PINWORMS

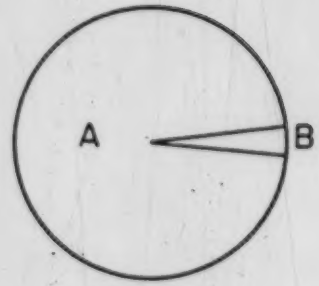
CEPHALURIS ALASKENSIS

HARD



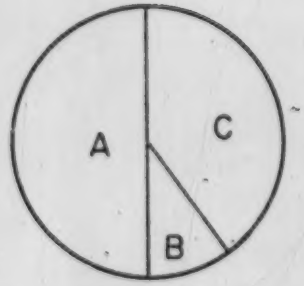
43 (11)

SOFT

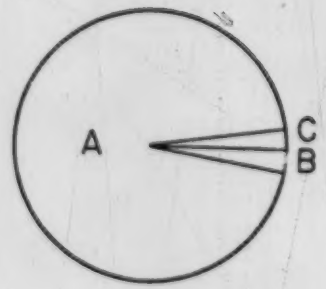


39 (7)

CEPHALURIS COLORADENSIS



68 (12)



38 (8)

faeces, or select prospective hard faeces. Schad (1963) investigated the site selection of eight species of pinworms (*Tachygonetria*) in the colons of tortoises (*Testudo graeca*) using a quick-freeze technique. He found four pairs of species, each of which had a different longitudinal distribution. He then studied the radial distribution, and discovered that one species of each pair tended to be a lumenal and the other a paramucosal dweller. In the present study, *Cephaluris* spp. in *O. princeps* overlap with both *Eugenuris* species A and *L. coloradensis* at different times, but appear to be cueing on properties of the lumen, while the latter species cue on properties of the gut wall. This suggests that *Cephaluris* spp. may be lumen dwellers, and the others paramucosal dwellers.

The situation in *O. collaris* is more puzzling. Not only do both species of *Cephaluris* migrate together, but *Eugenuris talkeetnaeuris* joins them. Only *L. rauschi* is sedentary in Zone C. Perhaps these species are segregated on food preferences. Alternatively, co-existence could occur if each species were principally limited by a different micronutrient, as may be the case for phytoplankton assemblages (Petersen, 1975).

Holmes (1973) and Crompton (1973) have recently reviewed the literature on helminth migrations. *Hymenolepis diminuta* is known to undergo forward migration in response to food in the host's stomach. Williams et al. (1970) recorded several examples of feeding migration of helminths

in rays and cod, and Mackenzie and Gibson (1970) noticed one example in plaice. These examples are perhaps atypical because the fish were brought into the laboratory and starved for some days to bring about a posterior migration. The example in pikas appears to be the first known case of a naturally occurring feeding migration of a gastrointestinal helminth. Other helminths should be similarly investigated; the phenomenon may be widespread.

CHAPTER VIII

ZOOGEOGRAPHY

Dawson (1967) reviewed the fossil record of lagomorphs during Tertiary. The earliest known ochotonids are *Desmatolagus gobiensis* and *Sinolagomys* sp., from the mid-Oligocene of Asia. By the Miocene, ochotonids were more diverse than leporids, and many species were present in North America. The North American ochotonid lines are thought to have become extinct, and the present species are all derived from Asian ancestors.

Ochotona, the only living genus of the family, arose in the Palaearctic Region, probably during Pliocene time, and apparently soon spread to the Nearctic Region. *Ochotona spanglei*, from a Hemphillian assemblage (Pliocene) in Oregon, is the first known Nearctic representative of the genus (Shotwell, 1956).

Records in the Pleistocene do not appear until Kansan time, with a giant pika *O. whartoni*, in Alaska (Guthrie and Matthews, 1971). Another giant pika, *Ochotona* sp., found in the Yukon Territory, is thought to be of late Sangamon age (Irving and Harington, 1973). North American records of pikas indistinguishable from living species, first appear in Illinoian cave deposits of Maryland (Gidley and Gazin,

1938); a mummified pika, *O.* cf. *collaris*, in Alaska is probably of Wisconsin age (Guthrie, 1973).

The current hypothesis concerning the present North American distribution of *Ochotona*, is that the two species are derived from a single migration across Beringia in Illinoian time, followed by a southerly spread along the Rocky Mountains, and a subsequent splitting into two groups due to the joining of the Cordilleran and Laurentide ice sheets in the Wisconsin (Rausch, 1974). The ancestral species must have spread south during a period when the ice sheets were not confluent, either late in Illinoian time or in Sangamon time. The presence of a fossil *Ochotona* resembling *O. princeps* in Maryland, in a deposit thought to be of Illinoian age, indicates that the spread must have been early and rapid. Presumably, since modern North American pikas are talus dwellers, the spread to the east must have been along patches of glacial drift. The pika in Maryland is somewhat anomalous in that Illinoian drift deposits were relatively fine-grained, unlike Wisconsin deposits (Flint, 1971: 559), which were rocky and should have provided more suitable habitat for pikas.

The records of giant pikas in Alaska and Yukon probably represent a line which probably became extinct during Wisconsin time, and is not related to extant pikas. The Yukon specimen was found in association with human artefacts. Humans have been suspected of causing extinction of other mammalian species in North America at this time (Hopkins,

1967; Martin, 1973), and may have been responsible for the extinction of the giant pika.

Rausch (1960, 1963a, 1963b) used evidence from helminth distributions to hypothesize a closer relationship of *O. collaris* to Asian pikas than to *O. princeps*. At that time, neither *Eugenuris* nor *Labiostomum* was known from *O. princeps*, and *Schizorchis caballeroi* was known only in *O. collaris*. Additional evidence was available from flea distributions (Holland, 1963): *Monopsyllus tolli*, a species found on Asian pikas, was known from *O. collaris*, but not from *O. princeps*.

Rausch later changed his hypothesis as more information became available on helminth distributions (Rausch and Ohbayashi, 1974), and karyotypes of pikas (Rausch and Ritter, 1973; Vorontsov and Ivanitskaya, 1969; Hayata and Shimba, 1970). Affinities of *O. collaris* and *O. princeps* to their geographically and ecologically closest congeners *O. hyperborea* and *O. alpina* are apparently remote, compared with their affinities to each other.

Ivanitskaya (1973), has found that *O. pusilla*, the steppe pika, has a chromosome number similar to that of *O. princeps*. She postulates that *O. pusilla* was in Beringia during the early Pleistocene, and is the ancester of *O. princeps*. Considering the present strict habitat requirements of *O. princeps* and *O. collaris* for talus, it seems more likely to me that the North American species have a common ancestry with a talus dweller (*O. hyperborea*, *O. alpina*,

O. rutila) rather than a steppe dweller, although a talus dweller would find little available habitat on Beringia.

I have found a great faunal similarity between the helminths of *O. collaris* and *O. princeps*. Three helminth species (*Cephaluris alaskensis*, *C. coloradensis*, and *Schizorchis caballeroi*) are common to these pikas, and two genera (*Labiostomum* and *Eugenuris*) are represented by species pairs, of which one member is in each species of pika. The major faunal difference is the absence of the trichostrongyloids *Graphidiella* and *Murielus* from *O. collaris*.

The distribution of *Schizorchis* spp. in North American pikas is the most difficult to fit into the current hypothesis concerning the origin of these pikas. A species not found in this study, *S. ochotonae*, has been reported from *O. princeps* in several localities in North America (see p. 20), but confirmed only in Colorado and Wyoming (R.L. Rausch pers. comm.). *Schizorchis caballeroi* is known from *O. collaris* in Alaska and Yukon Territory, and from *O. princeps* in Oregon and Alberta (see p. 20). Specimens of *S. caballeroi* are closer morphologically to specimens of the Asian species, *S. altaica*, than to those of *S. ochotonae*. This situation could possibly be caused by a complicated history of isolation and rejoining of populations since Illinoian time. Considering the present islandic distribution of pikas, this explanation seems reasonable. However, the distributions of species of other genera do not suggest such a history. A more critical examination of the variation

in *Schizorchis* within and between populations of *O. princeps* is required.

Distributions of species of *Graphidiella* and *Murielus* shed little light on the evolution of North American pikas. Presumably, both these genera were present previously in the *O. collaris-O. princeps* ancestor, and have since become extinct in *O. collaris*, at least in the populations surveyed. Both genera are represented in Asia. *Graphidiella olsoni* is known only from a small geographical area (Altai and Sayan Mountains) in *O. alpina* and *O. daurica*. No other species are known in the Palaearctic Region. *Murielus* is represented by three species in the Palaearctic Region, including *M. harpespiculus*, known also from *O. princeps*. This species has been found in *O. hyperborea*, the range of which extends closest to North America.

The distribution of the pinworms *Labiostomum* and *Eugenuris* support the hypothesis that both *O. princeps* and *O. collaris* are derived from the same Palaearctic ancestor. *Labiostomum rauschi* in *O. collaris*, and *L. coloradensis* in *O. princeps* are about as similar to each other as to the eastern Palaearctic species *L. vesicularis*. The same pattern applies to the *Eugenuris talkeetnaeuris* - *Eugenuris* species A - *E. schumakovitschi* group.

Cephaluris spp. distributions are the most consistent with the hypothesis. There are two easily distinguishable groups of species in this genus. Hobbs (in press) found two species of *Cephaluris*, one from each of the two groups, in

three of four host species studied (*O. princeps*, *O. collaris*, *O. rutila*). The Nearctic *Cephaluris alaskensis* is in the same group as the Palaearctic *C. andrejevi*; and *C. coloradensis* and *C. ochotonae* are in the other group. Unlike *Labiostomum* and *Eugenuris*, neither *Cephaluris coloradensis* nor *C. alaskensis* has undergone speciation since the splitting of *O. collaris* and *O. princeps*. However, these species and their Palaearctic counterparts must have diverged before the *O. collaris* - *O. princeps* split, implying a considerable period of separation of the Palaearctic - Nearctic lines. This is supported by karyotypic evidence. *Ochotona hyperborea* and *O. alpina*, which are considered the closest relatives of the living North American pikas (Rausch, 1974), have a different chromosome number (2n = 40; Hayata and Shimba, 1970; Vorontsov and Ivanitskaya, 1969) from *O. collaris* (2n = 68; Rausch and Ritter, 1973) or *O. princeps* (2n = 68; Adams, 1971; Wurster et al., 1971; Hsu and Benirschke, 1971; Wiseley, 1973).

Distribution patterns of fleas are more difficult to interpret, because they are not as host specific as helminths in pikas, and may be transported by other hosts. Pikas are primary hosts to three species in North America: *Monopsyllus tolli*, *Amphalius necopinus*, and *Ctenophyllus terribilis*. The latter two are found on both *O. collaris* and *O. princeps* (Holland, 1963), although I did not find either on *O. collaris* in the Yukon. Both fleas have related species (*A. runatus* and *C. armatus*) in the Palaearctic Region, so similar to them,

that differences may be only at the subspecific level (Holland, 1958, 1963). *Monopsyllus tolli* is known on *O. collaris* in the Nearctic Region and also on eastern Palaearctic pikas. It may have been present on *O. princeps* and become extinct, or more likely, it may represent a more recent invasion to the Nearctic Region via another mammal, after the splitting of *O. collaris* - *O. princeps*.

In conclusion, the parasite distribution data are consistent with the hypothesis that *O. collaris* and *O. princeps* are derived from a single migration of a Palaearctic ancestral species, probably during the Illinoian glaciation. There is some evidence from parasites that the *O. collaris* - *O. princeps* pair diverged from its Palaearctic ancestor as a single unit on North America before diverging into the two extant descendant species.

CHAPTER IX

CONCLUDING DISCUSSION

Helminths of pikas must have had a long evolutionary history together; none of those encountered in this study appears to be new to pikas, as no species have congeners in hosts other than pikas. The pinworms form a monophyletic group as evidenced by the similarity of cloacal papillae in males (Figure 18), and probably are derived from an ancestor common to *Dermatoxys* in leporids. My views on the phylogeny of these pinworms are shown in Figure 19. Each character state is designated by a letter: lower case is used for primitive condition, and capital for derived condition. A summary of characters is shown in Table 16. Reasons for assigning conditions to either primitive or derived for each character state are as follows:

Number of lips. Because the commonest state in this group is three lips, and because this state occurs in parasites of all host groups, it is designated as primitive. Additionally, those genera with six lips have them arranged in pairs.

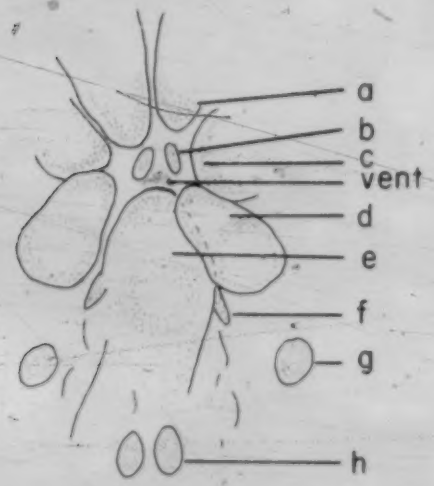
Precloacal ventral ornament. This transformation series is based on the assumption that the direction of evolution has been from a broad to a narrow ornament.

Table 16. Phylogenetic classification of character states of a group of pinworms belonging to the family Oxyuridae Cobbold 1864

Character	State			
	Primitive		Derived	
Number of lips	3	(a)	6	(A)
Precloacal ventral ornament	pseudosucker	(b)	crest consisting of a row of transverse teeth	(B^1)
			crest consisting of a laterally compressed ridge	(B^2)
Cushion-like cloacal papilla	absent	(c)	present	(C)
Cuticular ornamentation of anterior end	absent	(d)	cervical wings	(D^1)
			cephalic bulb	(D^2)
			lateral cephalic lobes and cuticular flange	(D^3)
			pair of dorsal cuticular shields	(D^4)

Figure 18. Diagrammatic representation of cloacal papillae in male pinworms. The papillae are labelled a-h, in order to show the similarity between genera.

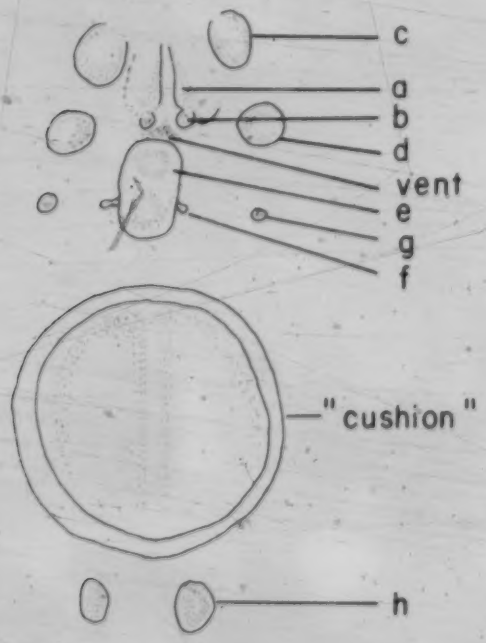
EUGENURIS species A



100 μ

LABIOSTOMUM RAUSCHI

CEPHALURIS ALASKENSIS



100 μ

CEPHALURIS COLORADENSIS

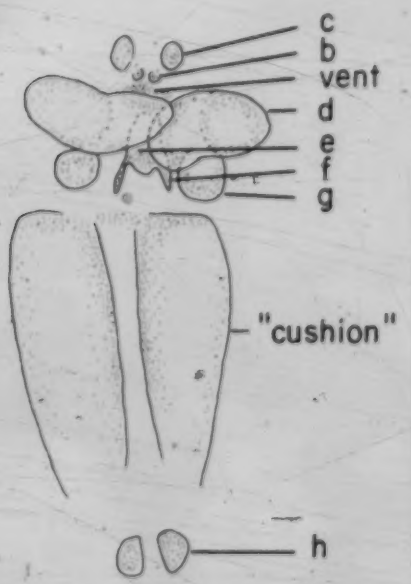
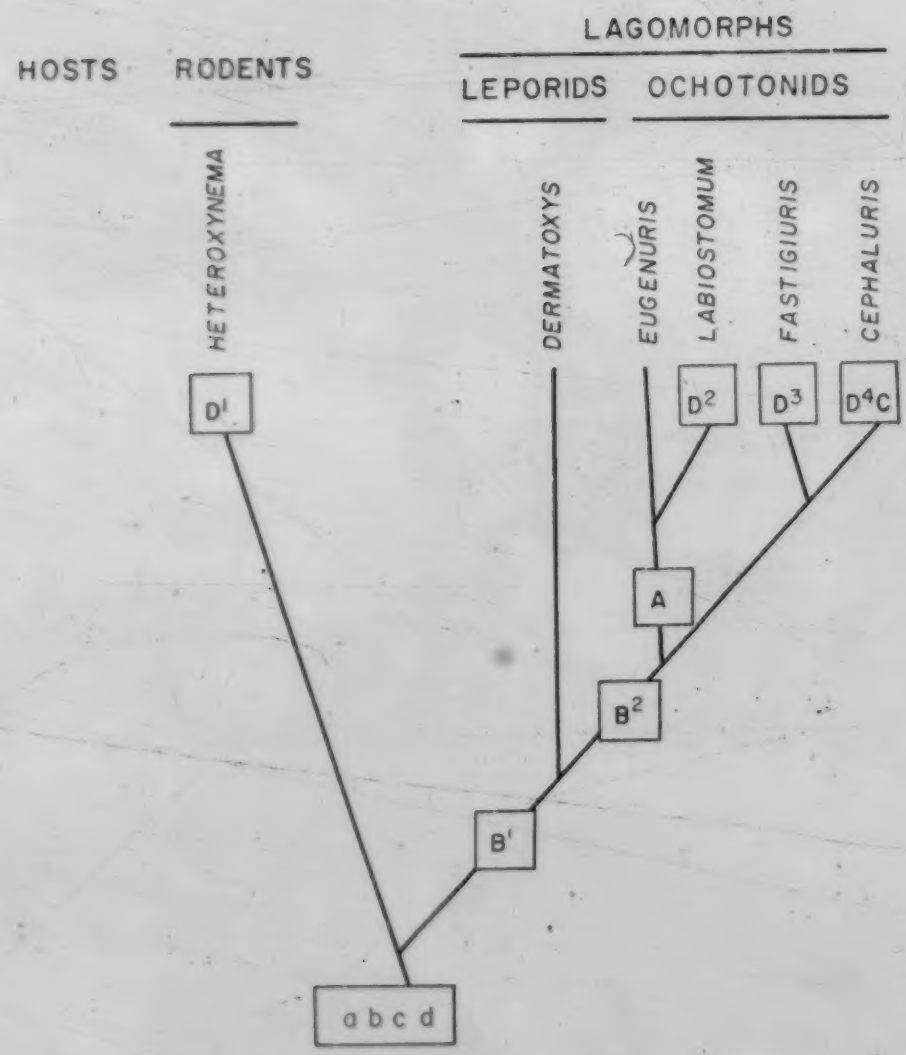


Figure 19. Diagram showing hypothetical phylogeny of a group of pinworms in the family Oxyuridae. See Table 16 for explanation of letters.


HOSTS
RODENTS
LAGOMORPHS
LEPORIDS
OCHOTONIDS
HETEROXYNEMA
DERMATOXYS
EUGENURIS
LABIOSTOMUM
FASTIGIURIS
CEPHALURIS
D¹
D²
D³
D⁴C
A
B²
B'
a b c d

The pseudosucker of the genus in rodents (*Heteroxynema*), is a relatively short and broad structure. I consider this to be primitive, because similar structures are present in several other genera of pinworms in rodents. All pinworms of this group which inhabit lagomorphs possess an elongated crest; only in those inhabiting pikas is the crest laterally compressed.

Cushion-like cloacal papilla. Because this is present in only one genus, I consider it to be a derived state.

Cuticular ornamentation of the anterior end. There is great variety exhibited by the pika pinworms in this character. Because the ornamented character states are not easily derived one from the other, I consider the un-ornamented state to be primitive.

Among the other genera inhabiting pikas in North America, *Graphidiella* does not have close affinities to any living genus, but is probably closest to *Graphidium*, the stomach worm of leporids. The heligmosome *Murielus* does not have any relatives in the Heligmosomidae, which is now believed to be a polyphyletic group (Durette-Desset, 1971). There are however, many similarities (e.g., synloph structure, dorsal ray arrangement, spicule shape) to the trichostrongylid genus *Nematodirus*, particularly to those species found in leporids (Dikmans, 1939; Durette-Desset, 1974). The cestode *Schizorchis* is the only genus which does not have a counterpart in leporids. Although it must have been in pikas at least before the Illinoian, considering its wide-

spread present distribution in them, it is perhaps the newest of pika helminths. It resembles *Monoecocestus*, parasites of many different groups of mammals in both the Old World and New World.

Pikas offer an excellent opportunity to study the structure of an old helminth community system. According to Holmes' (1973) hypothesis, individuals in such systems should show an avoidance of competitive exclusion by interactive and selective segregation. Data given above are consistent with the hypothesis. Indeed, those species which appear to have been in pikas longest (*Graphidiella* and the pinworms) are those which use selective site segregation, the kind considered by Holmes (1973) to be the most highly evolved. Species of *Schizorchis*, the most recent pika helminths, are those most affected by interactive site segregation, as expected.

Studies of this type tend to pose more questions than are answered. Several lines for future research became obvious during the course of this study. I shall briefly discuss four of these.

The distribution of *S. caballeroi* along the intestine needs to be studied experimentally. I had assumed during this study that small worms were young worms. However, I once found a small *S. caballeroi* in the intestine of a pika which had been in the laboratory for six months. The pika was very unlikely to acquire new infections in the laboratory. Eggs of *S. caballeroi* were numerous in the faeces of this

pika until three months before the host's death. It is possible then, that many of the small worms in field-collected pikas were not young. With care, it is possible to keep pikas in the laboratory for experimental studies, and even to breed them (Severaid, 1950; Underhill, 1962). A large number of captive pikas would be necessary to follow the distribution shifts of *S. caballeroi* in the small intestine at various ages of infection.

In order to carry out the above study, it would first be necessary to determine the intermediate host for *S. caballeroi* and to complete the life cycle. Other anoplocephalids use oribatid soil mites. Pika haypiles would provide good habitat for mites, and it may be profitable to study mites associated with haypiles. Indeed, there may well be modification of the behaviour of infected mites, such that they would be more likely to be ingested by the definitive host; a situation similar to that found for ants infected with *Dicrocoelium dendriticum* (reviewed by Carney, 1969) and gammarids infected with *Polymorphus paradoxus* (Bethel and Holmes, 1973).

Understanding is incomplete of site segregation by pinworms. The considerable overlap between preferred sites of *Cephaluris* spp. and *Eugenuris talkeetnaeuris* in *O. collaris* remains to be explained. Use of Schad's (1963) technique of rapidly freezing the gut in liquid nitrogen or alcohol/dry ice mixture (Hair and Holmes, 1975), so that lumenal and paramucosal dwelling worms can be separated, may prove profit-

able. Alternatively, it may be possible to develop an immunological technique for gut content analysis of the worms, to determine differences in feeding preferences, as has been done for turbellarians (Reynoldson and Davies, 1970).

This study was too short to adequately observe the dynamics of extinction and recolonization of helminths in the island-like populations of hosts. The patchy distributions of *Murielus harpespiculus*, and the different abundances of other species in various localities (see Chapter VI), indicate that a long-term study would be worthwhile. The northern part of the Alberta study area is an ideal place for such a study, as there are many semi-isolated pika populations of differing sizes and degrees of isolation.

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Appendix I. Samples sizes of pinworms measured for taxonomic comparisons. All worms were collected by the author, unless otherwise indicated.

Species	Host	Locality	Sex of Worm	Sample Size
Cephaluris alaskensis	*Ochotona collaris*	Yukon	Male	22
	Ochotona princeps	Kananaskis	Male	20
	Ochotona princeps	Colorado*	Male	10
Cephaluris coloradensis	*Ochotona collaris*	Yukon	Male	20
	Ochotona princeps	Kananaskis	Male	20
	Ochotona princeps	Sheep R.*	Male	10
	Ochotona princeps	Colorado*	Male	9
C. alaskensis-C. coloradensis	*Ochotona collaris*	Yukon	Female	23
	Ochotona princeps	Kananaskis	Female	20
	Ochotona princeps	Colorado*	Female	10
Cephaluris andrejevi	*Ochotona rutila*	Kazakhstan**	Male	10
			Female	7
	Ochotona hyperborea yesoensis	Japan***	Male	4
			Female	6
Cephaluris ochotonae	*Ochotona rutila*	Kazakhstan**	Male	1
			Female	8
Eugenuris talkeetnaeuris	*Ochotona collaris*	Yukon	Male	20
			Female	20
Eugenuris sp. A	*Ochotona princeps*	Kananaskis	Male	20
			Female	20
Eugenuris schumakovitschi	*Ochotona rutila*	Kazakhstan**	Male	7
			Female	7
Labiostomum rauschi	*Ochotona collaris*	Yukon	Male	20
			Female	20
Labiostomum coloradensis	*Ochotona princeps*	Kananaskis	Male	20
			Female	20
Labiostomum vesicularis	*Ochotona rutila*	Kazakhstan**	Male	2
			Female	4

* Courtesy of Dr. W.M. Samuel, University of Alberta.
** Courtesy of Dr. R.L. Rausch, University of Saskatchewan.
*** Courtesy of Dr. F.C. Zwickel, University of Alberta and Dr. H. Abe, Hokkaido University.

Appendix II. A. Measurements of female Eugenuris spp. from the literature. Measurements are in micrometres unless otherwise indicated

Structure	E. schumakovitschi		E. pikaeuris		E. talkeetnaeuris	E. havliki	Eugenuris utahensis
	Shul'ts 1948	Tokobaev 1960	Akhtar 1953	Barus et al. 1972	Akhtar 1956	Erhardova-Kotrla and Daniel 1970	Grundmann and Lombardi 1976
Length (mm)	12.4-18.0	15.0-17.0	19.05	18.1-20.9	18-21	17-24	15.9-18.5
Width	828-970	1189	1040	930-1060	840-1015	528-616	750-820
Striations			20		12		15-280**
Lateral alae width			10*		70		
Oesophagus length	1110-1470	1353-1394	1545	1040-1200	1603	968-1000	
Oesophagus bulb width	185-206	207-215		170-180			210-250
Buccal cavity depth	41		50	36-43	25		
Nerve ring	206		320	200-290	227		
Head diameter			180		148		
Tail (mm)	1.0		2.64	3.03-3.12	2.147	2.6-3.0	2.2-2.8
Distance of vulva from anterior end (mm)	4.84-7.06		9.06		9.625	7.9-10.0	6.77-7.69
Egg length	83-90	99-107	90-100	87-92	120	123	100
Egg width	50-54	49-58	40-50	43-47	60	52-57	50

* This is probably a typographical error, and may represent 100 micrometres

** A typographical error, probably 15-28 micrometres

Appendix II (Continued). B. Measurements of male Eugenuris spp. from the literature. Measurements are in micrometres unless otherwise indicated

	E. schumakovitschi		E. pikaeuris		E. talkeetnaeuris	E. havliki	Eugenuris utahensis
	Shul'ts 1948	Tokobaev 1960	Akhtar 1953	Barus et al. 1972	Akhtar 1956	Erhardova-Kotrla and Daniel 1970	Grundmann and Lombardi 1976
Length (mm)	8.6-11.0	9.0-10.0	7.85	10.1-10.6	10.1-11.8	11.0-14.0	8.0-11.6
Width	453-494	779	520	490-620	375-438	440-484	320-570
Striations		8.3	10		12		
Lateral alea width		58	50		61		
Oesophagus length	756-864	943-984	850	760-870	984	768-880	
Oesophagus bulb width				120-130			140-160
Buccal cavity depth			300*	32-360**	18		
Nerve ring			130	250-310	172		
Head diameter			110		105		
Tail length (from cloaca)	587-639	481-514	1350	540-600	700	700-790	470-620
Tail tip (from caudal alae)	154	124-149					
Distance from anterior end of ventral ridge to cloaca			1810		1768		

* This is probably a typographical error, and may represent 30 micrometres

** A typographical error, probably 32-36 micrometres

Appendix III. A. Measurements of female *Labiostomum* spp. from the literature. Measurements are in micrometres unless otherwise indicated

Species	*L. naimi*	*L. rauschi*	*L. vesicularis*	*L. akhtari*	*L. coloradensis*	"*Eugenuris* sp."
Source	Akhtar 1941	Akhtar 1956	Gvozdev 1956	Inglis 1959	Leiby 1961	Spasskii & Ryzhikov 1951
Length (mm)	14.96	18.23	1.4-1.5*	9.5-16.0	17.2-21.6	19.9
Width	445	750	720-740		670	770
Striations		18	21			25
Lateral alae width		36				
Oesophagus length	1333	969	1360-1400	1000-1500	1340	1540
Oesophagus bulb width	143		160-200		182	240
Buccal cavity depth			300-320			
Nerve ring		180	220			
Head diameter			90-100			126
Cephalic bulb diameter	290	240	220-240		195	390
Tail (mm)	1.24	1.07	1.44-1.50	1.1-1.9	1.80	
Distance of vulva from anterior end	6.87	9.0	5.4-6.6	4.5-8.0	7.8	9.6
Egg length	90	97-104	88-90	85-95		
Egg width	43	50-56	44-46	38-42		

* This is probably a typographical error, and may represent 14-15 mm

Appendix III (Continued). B. Measurements of male *Labiostomum* spp. from the literature. Measurements are in micrometres unless otherwise indicated

Species	*L. naimi*	*L. rauschi*	*L. vesicularis*	*L. akhtari*	*L. coloradensis*
Source	Akhtar 1941	Akhtar 1956	Gvozdev 1956	Inglis 1959	Leiby 1961
Length (mm)	3.4	12.0	9.0-10.0	7.5-9.0	3.5
Width	283	425	500		420
Striations		18			
Lateral alae width		32			
Oesophagus length	832	885	1020-1060	750-850	780
Oesophagus bulb width	130	120	130-140		117
Buccal cavity depth		127			
Nerve ring		140			
Head diameter			80-90		
Cephalic bulb diameter	245	180	220-240		
Tail length (from cloaca)	436	600	460-520	350-450	355
Distance from anterior end of ventral ridge to cloaca		1365			930